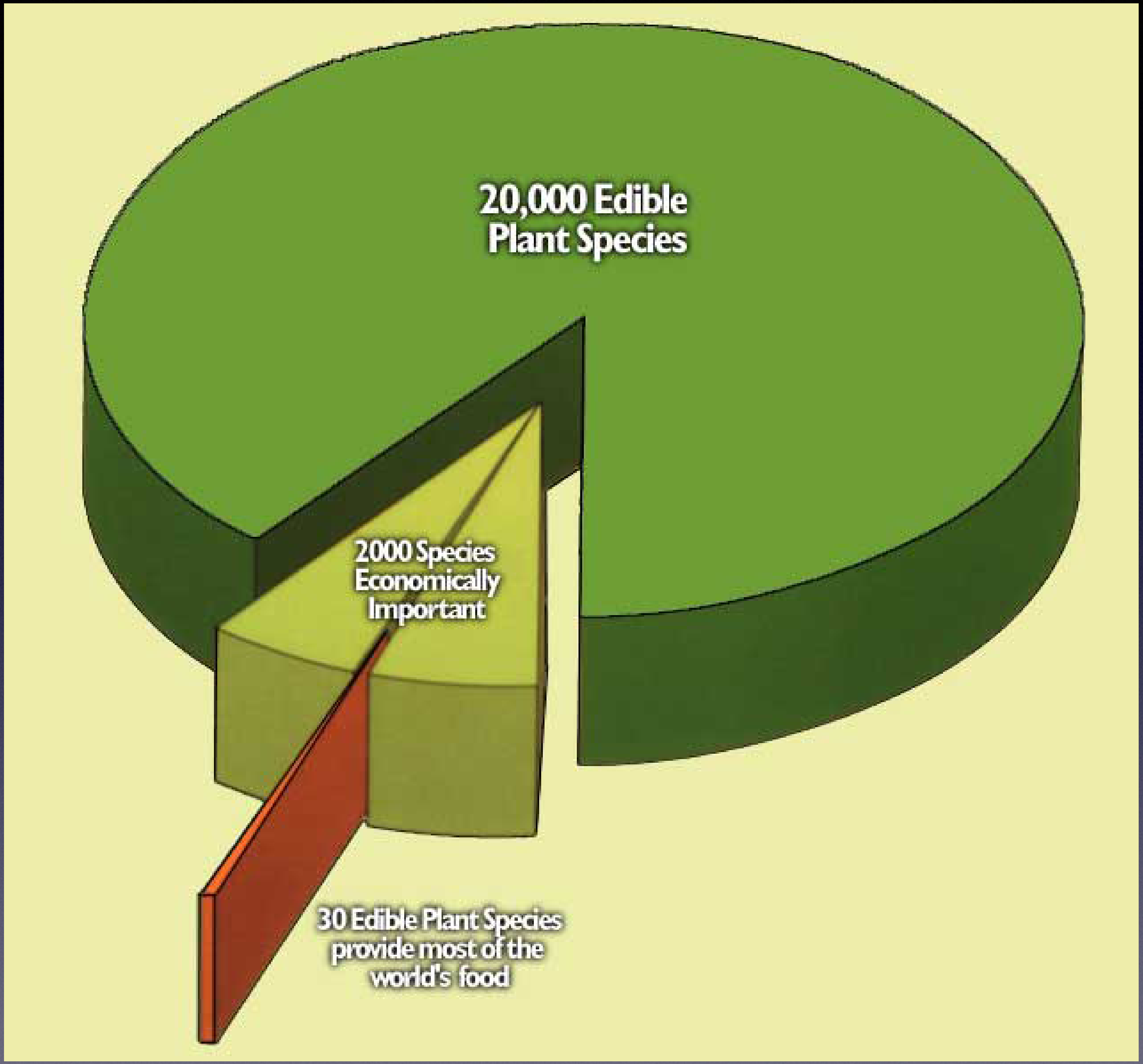
Extended material:
Crop traits
(not directly examinable)

NST PMS 1B

~400,000 plant species (http://www.theplantlist.org)



3 crop species (rice, wheat and maize) provide 60% of all calories and 54% of all protein in human food

120 cultivated plant species

Wild watermelon

Originated in North Africa, used as a primitive water carrier. Selection for sweeter taste was linked to pink colour of the flesh.

Modern watermelon

Over time, humans have bred watermelons to have a **bright red**, juicy interior. The **seeds are often removed** by preventing the plants from being fertilized by pollination.

Wild banana

The first bananas may have been cultivated at least **7,000 years ago** in what is now Papua New Guinea, and were **stocky and hard,** with large, tough **seeds** throughout the fruit's interior.

Modern banana

Today's tastier bananas are **hybrids** of two wild banana varieties, **Musa acuminata** and **Musa balbisiana.**

Wild eggplant

Eggplants once came in a wide array of shapes and colors, from **blue to yellow,** and some were **round** rather than oblong. Primitive eggplant varieties had a **spine** where the modern plant's stem connects to its flowers.

Modern eggplant

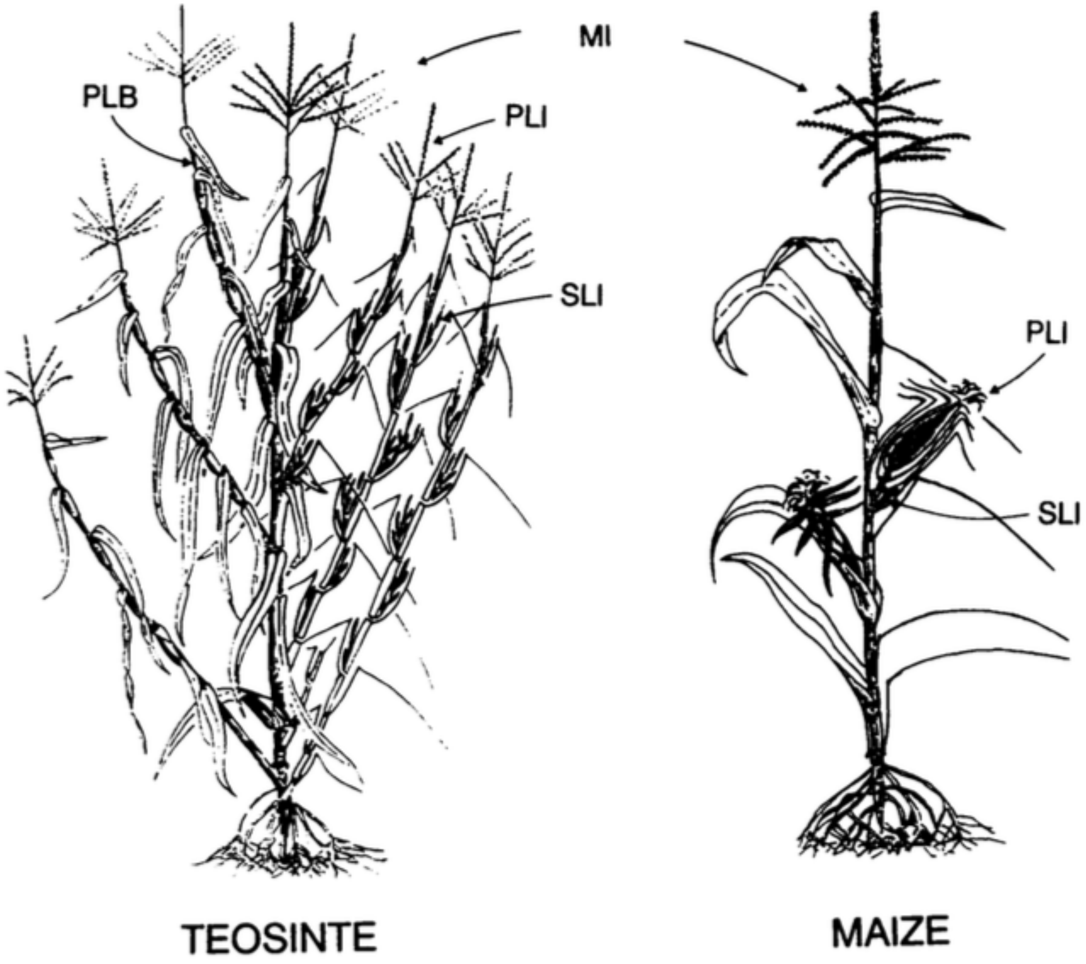
Selective breeding has made the **spine disappear** and left us with the **oblong purple** vegetable we're familiar with.

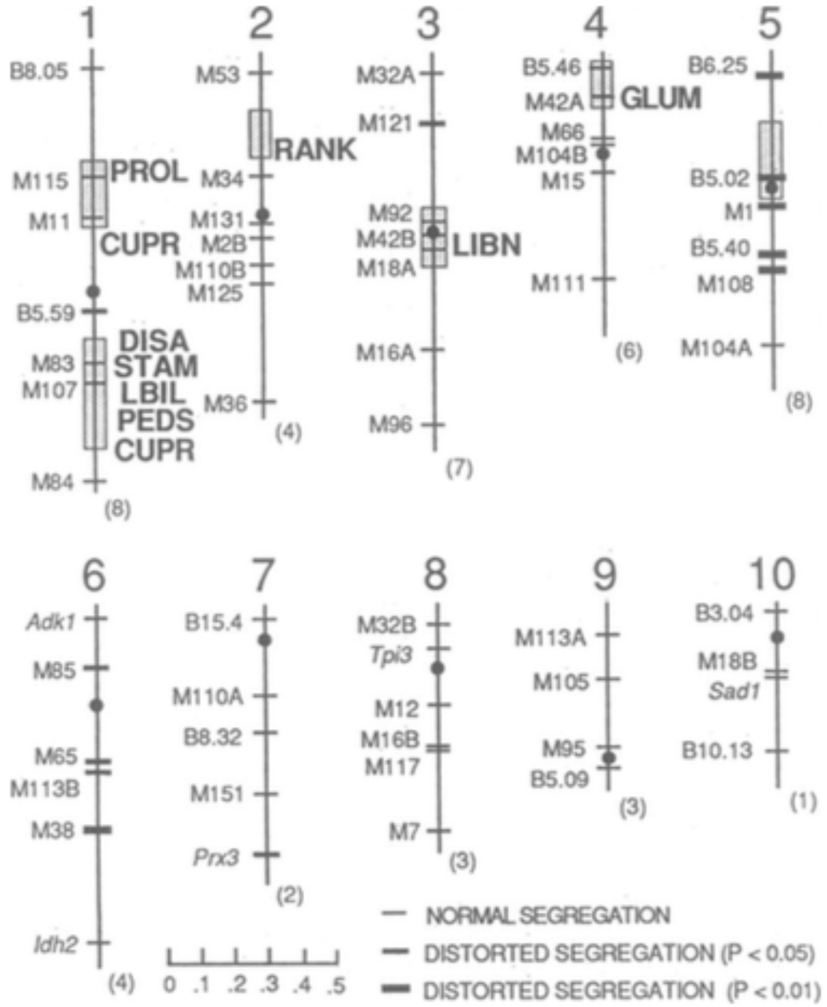
Wild carrot

The first carrots were likely cultivated around the 10th century in Asia Minor and were either **white or purple** with thin, forked roots and a **strong flavor.**

Modern carrot

Carrots today are large, **bright orange,** and tasty.





Major differences between maize and teosinte map to few loci

Table 1. List of principal traits distinguishing maize and teosinte

Trait	Description
CUPR (cupules per rank)	Number of cupules in a single rank
DISA (disarticulation score)	Tendency of ear to shatter (1–10 scale)
GLUM (glume score)	Hardness and angle of outer glume (1–10 scale)
LBIL (lateral branch internode)	Average length of internodes on the primary lateral branch
LIBN (branch number)	Number of branches in primary lateral inflorescence
PEDS (pedicellate spikelet score)	Percentage of cupules lacking the pedicellate spikelet
PROL (prolificacy)	Number of ears on the primary lateral branch
RANK (rank)	Number of rows of cupules
STAM (staminate score)	Percentage of male spikelets in primary lateral inflorescence

Doebley *et al*., PNAS (USA) 87: 9888-9892 (1990)

Crop traits

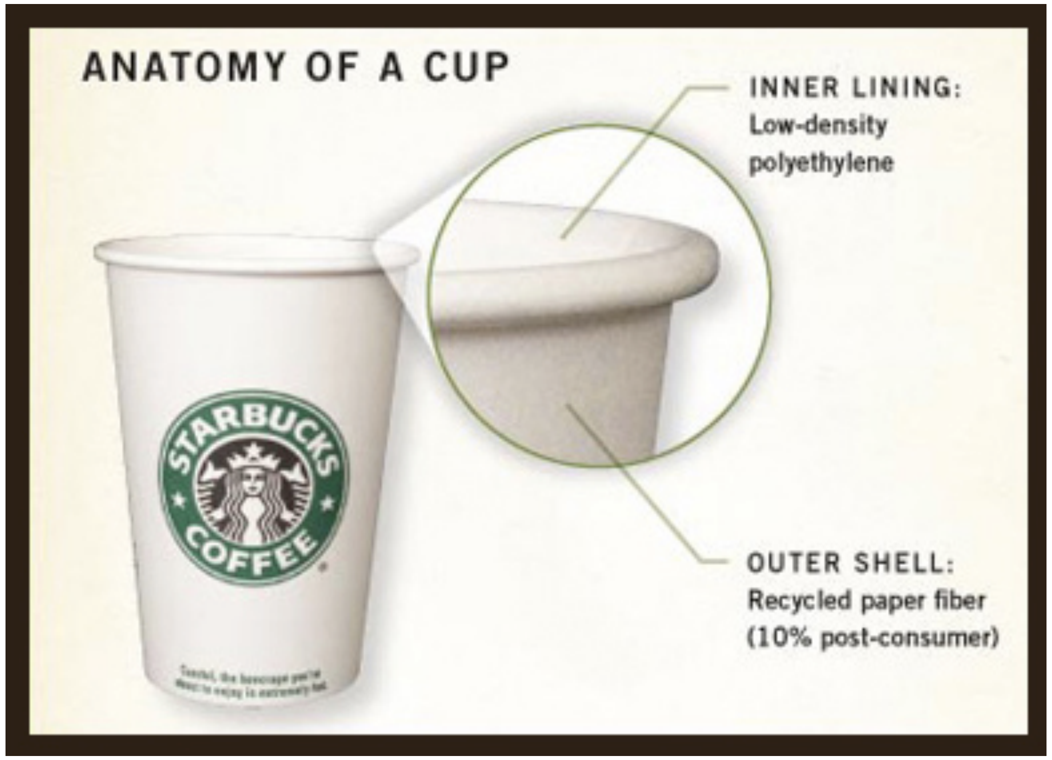
Traits that have been selected for by humans include:

- Determinate growth habit (flowering occurs at the top of the plant, preventing further growth)
- Synchronous ripening, shorter maturity
- Lower content of bitter tasting and harmful compounds
- Reduced sprouting (higher seed dormancy)
- Improved harvest index (the proportion of the plant which is used); larger seed or fruit size
- Elimination of seeds, such as in banana
- Retention of mature seed on the plant (loss of grain shattering)

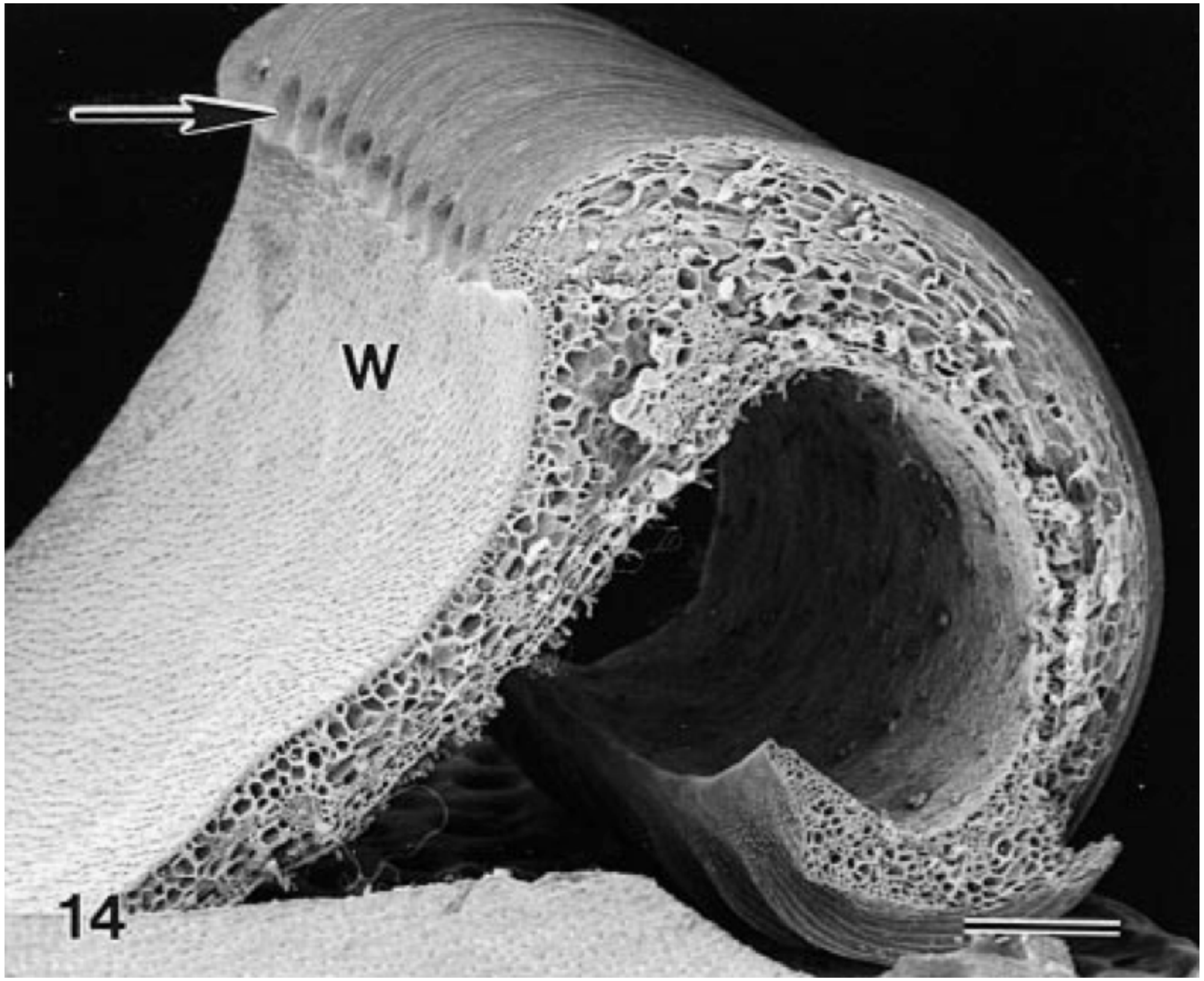
Many of these traits are multigenic and affect the shape and function of plant tissues and organs. If we want to engineer new crop traits in the future, we will need to understand the way DNA code is able to regulate plant growth and form.

BBC Natural History Unit


CAUTION: VERY HOT
Decaf
Milk
Shots
Custom
Syrup
Drink
Careful, the beverage you're about to enjoy is extremely hot.



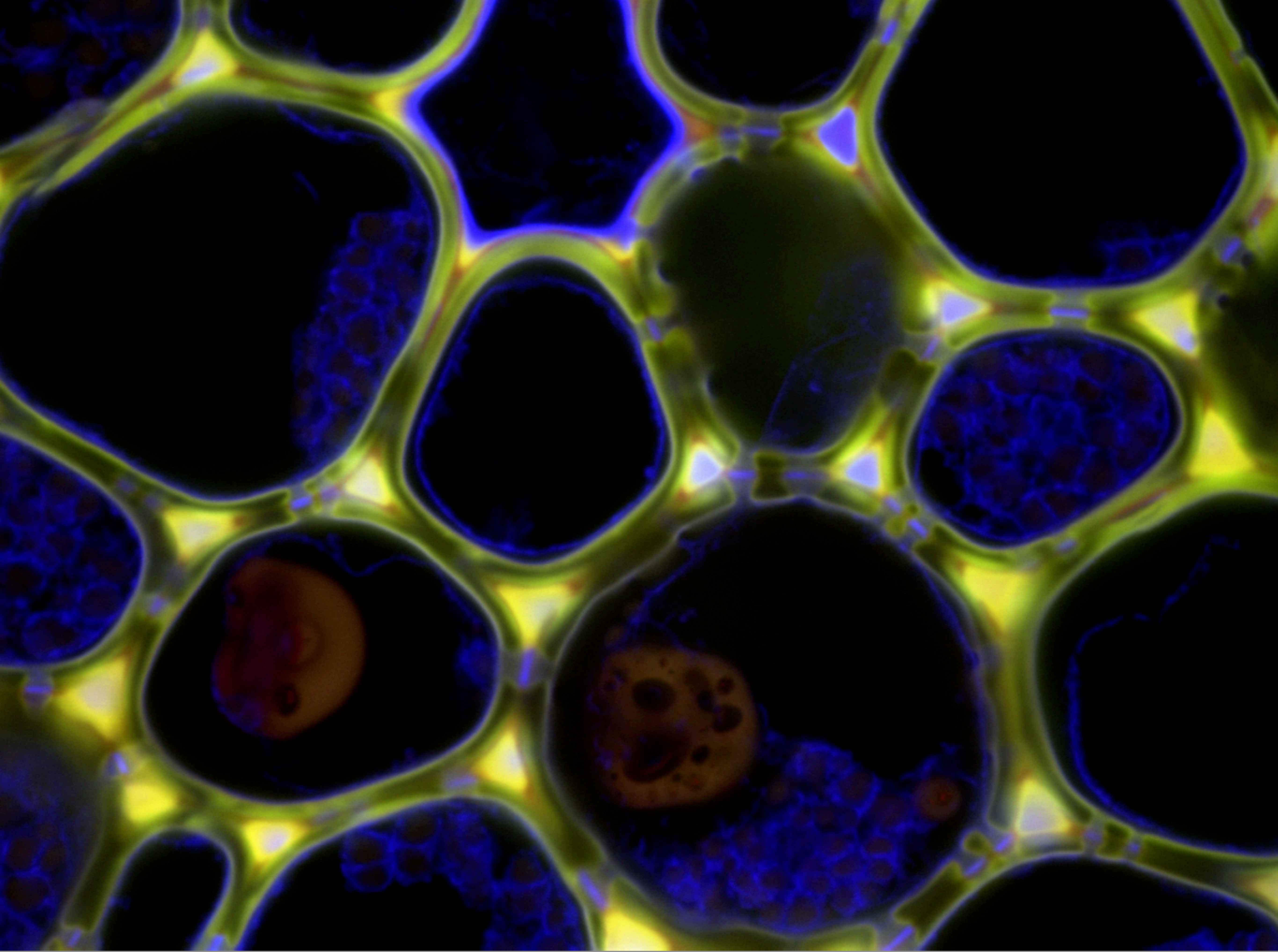
paper cup



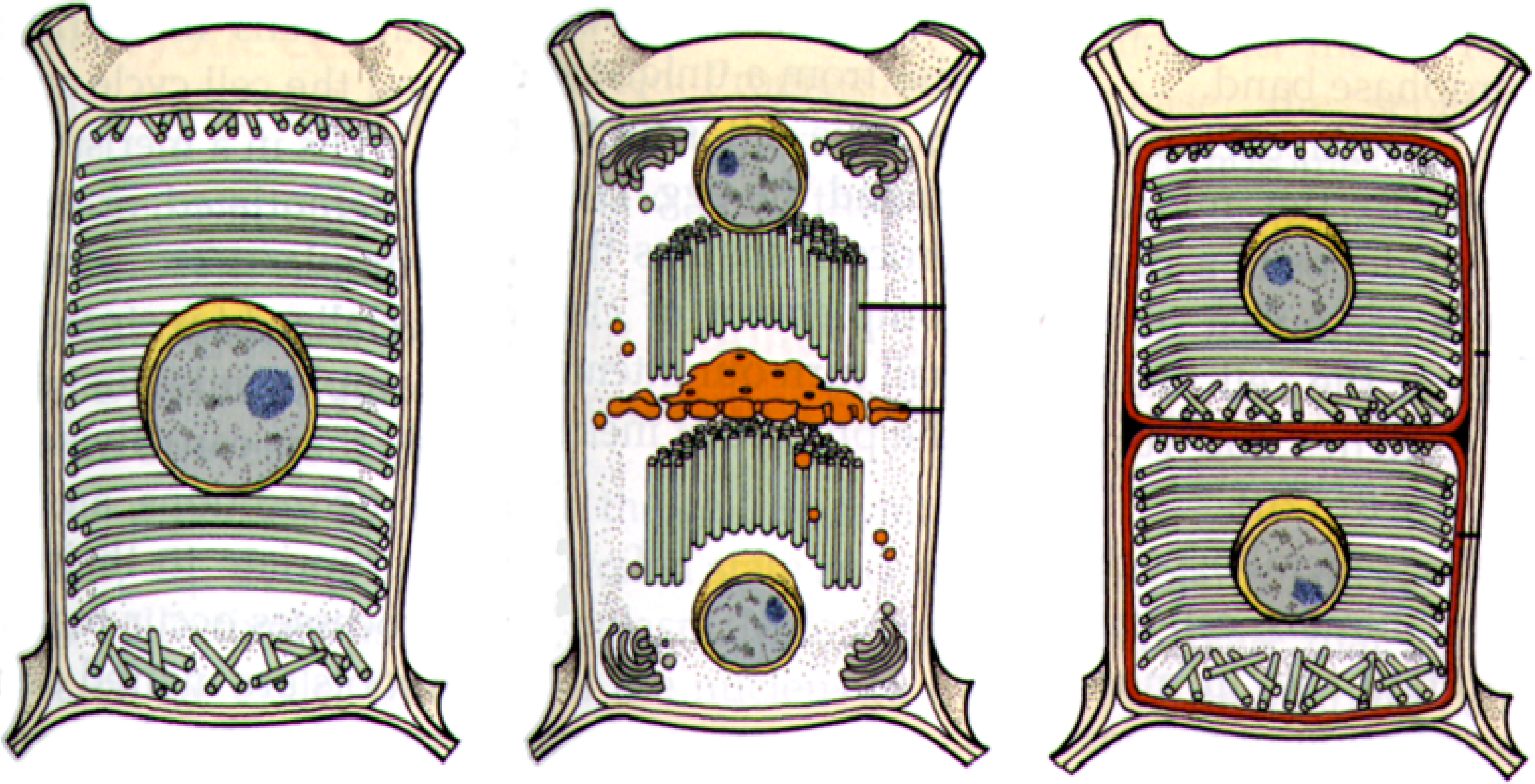
pitcher plant

sarracenia.com

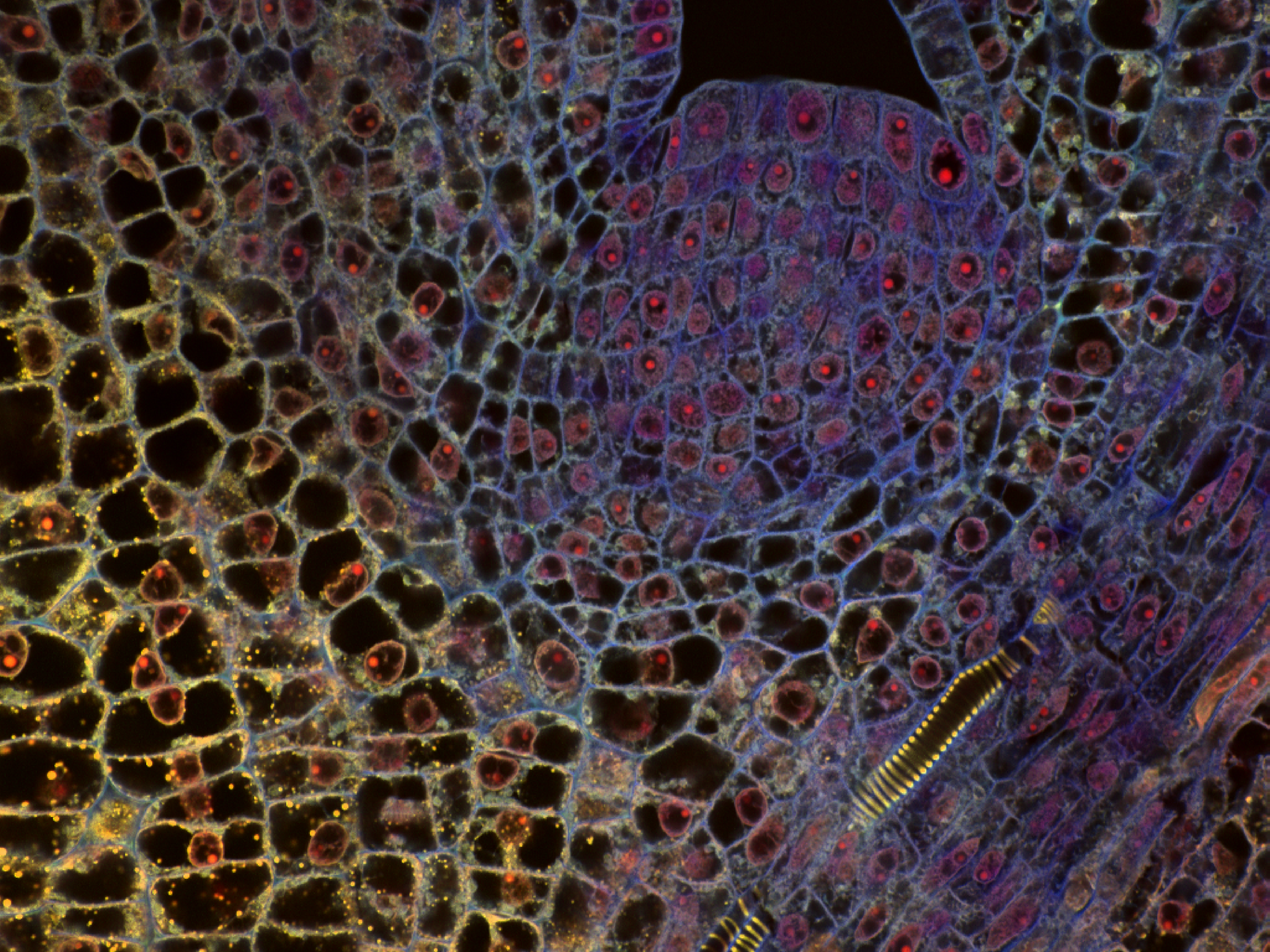
© 2009 Alastair Robinson

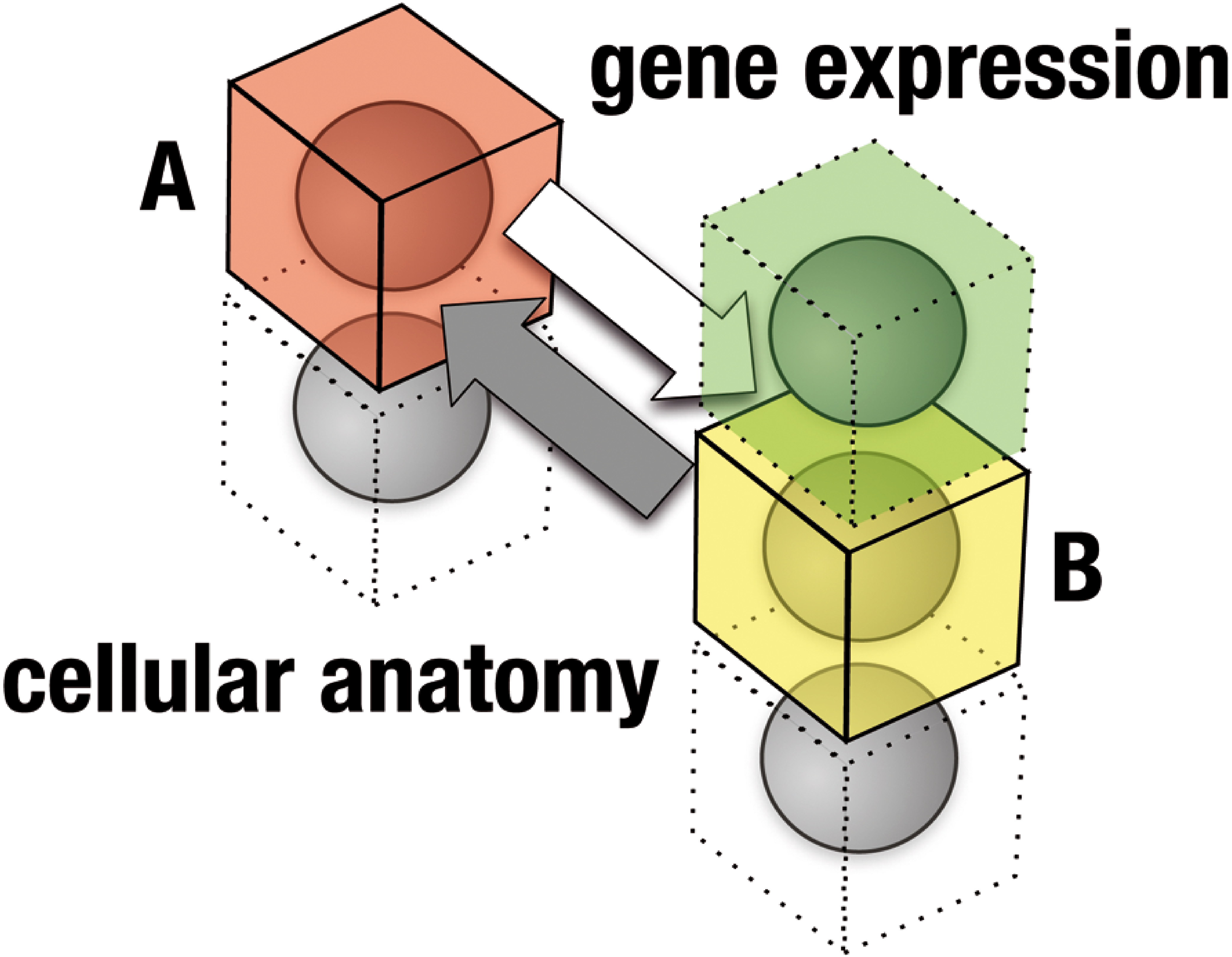


Plant cells are immobilised.
Morphogenesis is driven by cell division and elongation.



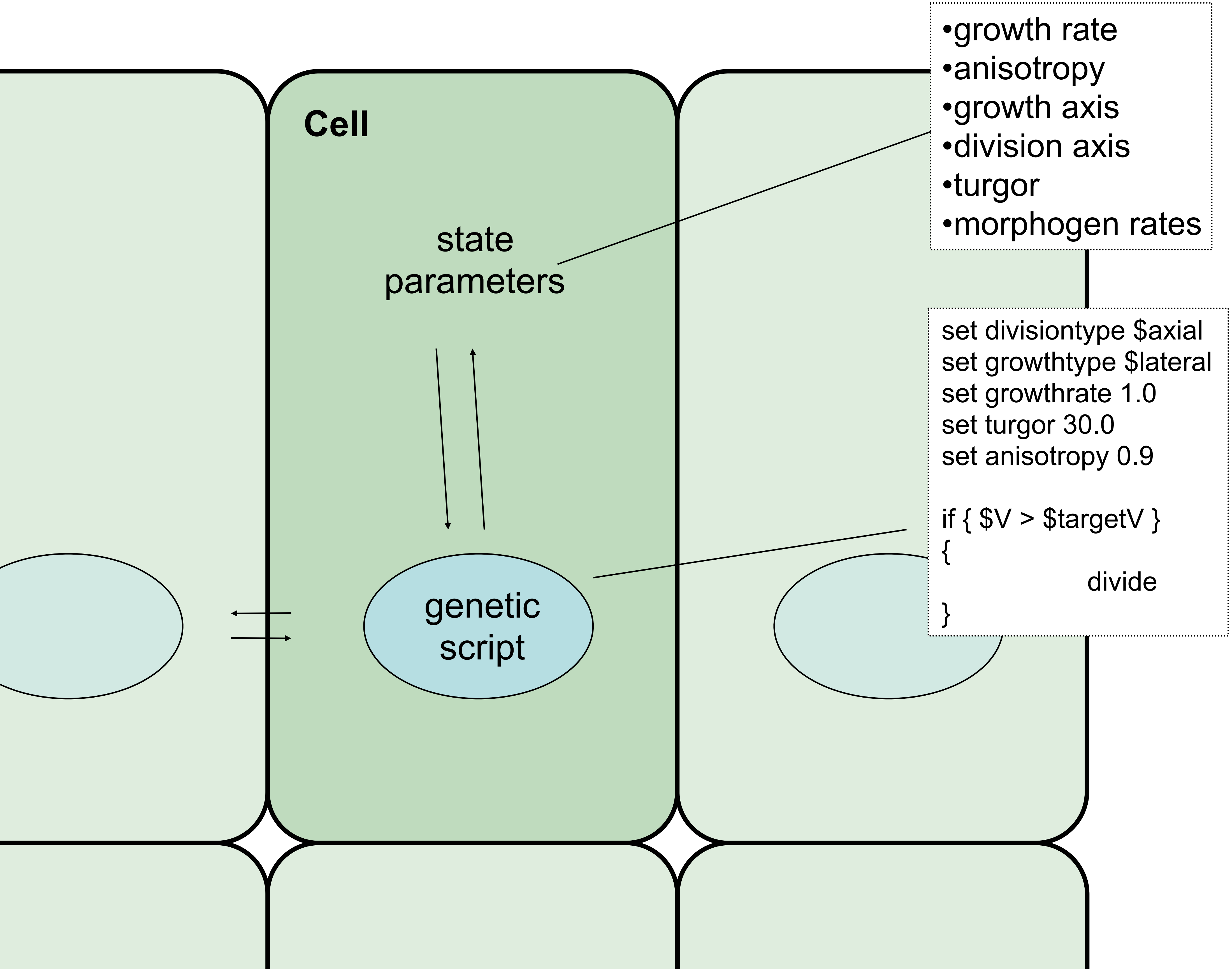
Cells are the common unit for gene expression





Self-organisation is driven by cellular interaction and feedback

Cellular automata models for plant morphogenesis



Cell

state parameters

genetic script

- growth rate
- anisotropy
- growth axis
- division axis
- turgor
- morphogen rates

physical model

```
set divisiontype $axial
set growthtype $lateral
set growthrate 1.0
set turgor 30.0
set anisotropy 0.9

if { $V > $targetV }
{
                divide
}
```

genetic model

Simple rules describe plant cell division

1. Hofmeister's rule (1863)
Cell plate formation normal to the growth axis.

2. Sachs' rule (1878)
Cell plate formation at right angles to existing walls.

3. Errera's rule (1888)
Cell plate of minimal area for cutting the volume of the cell in half.

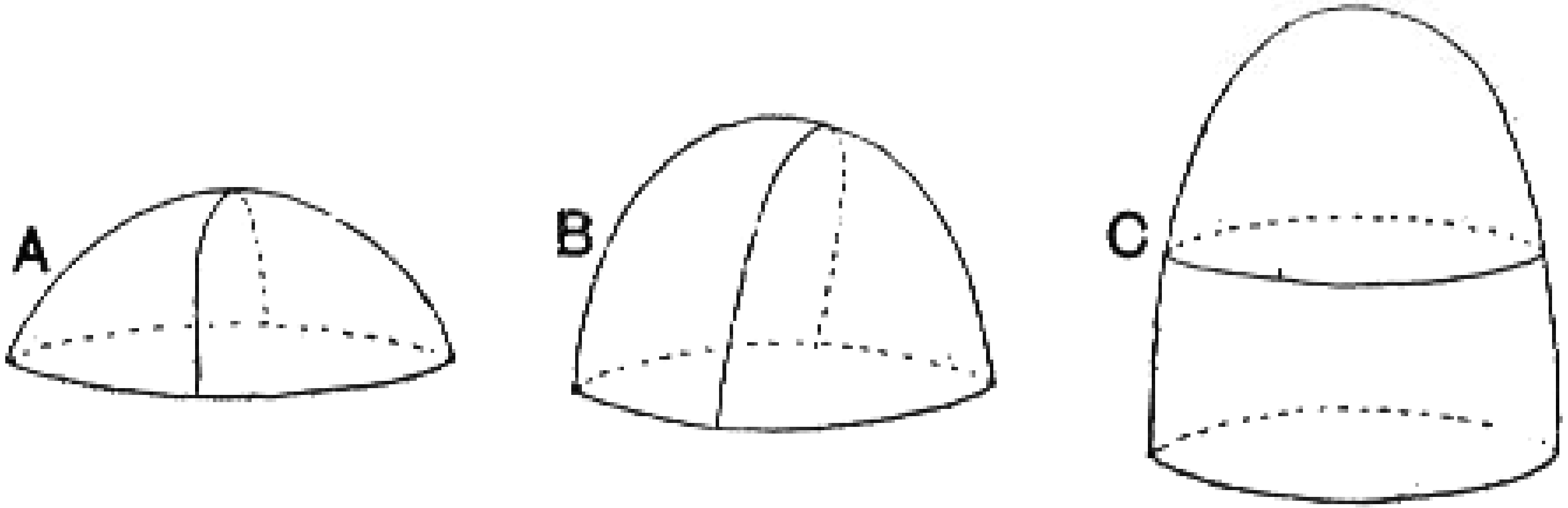
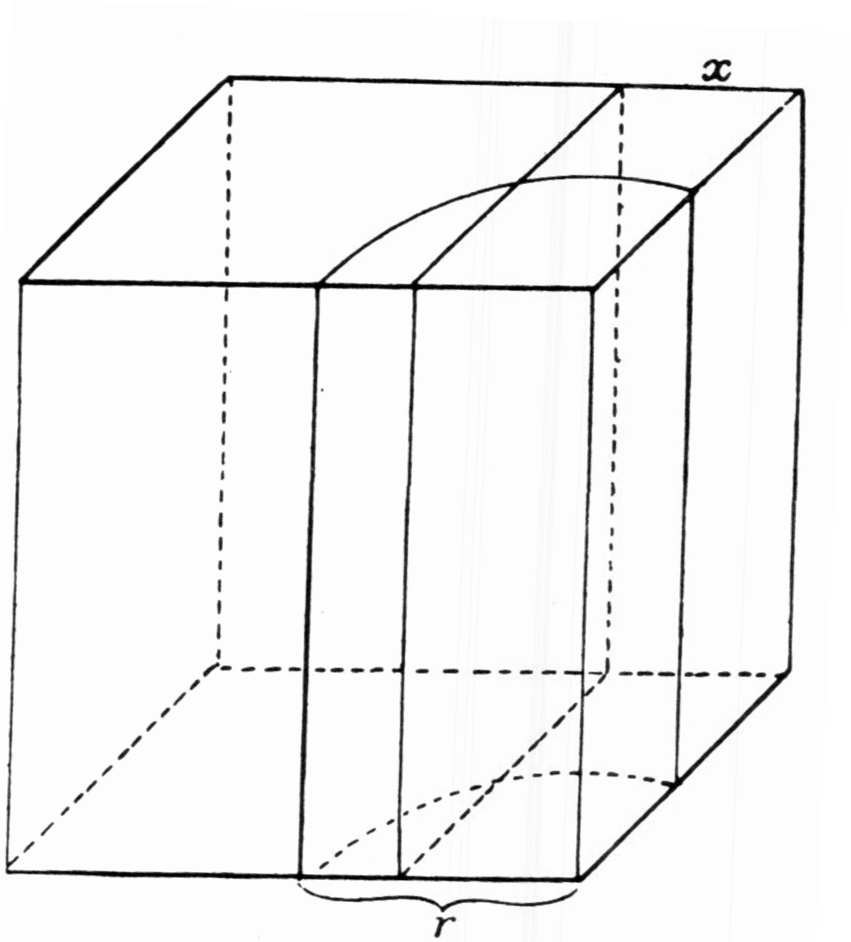
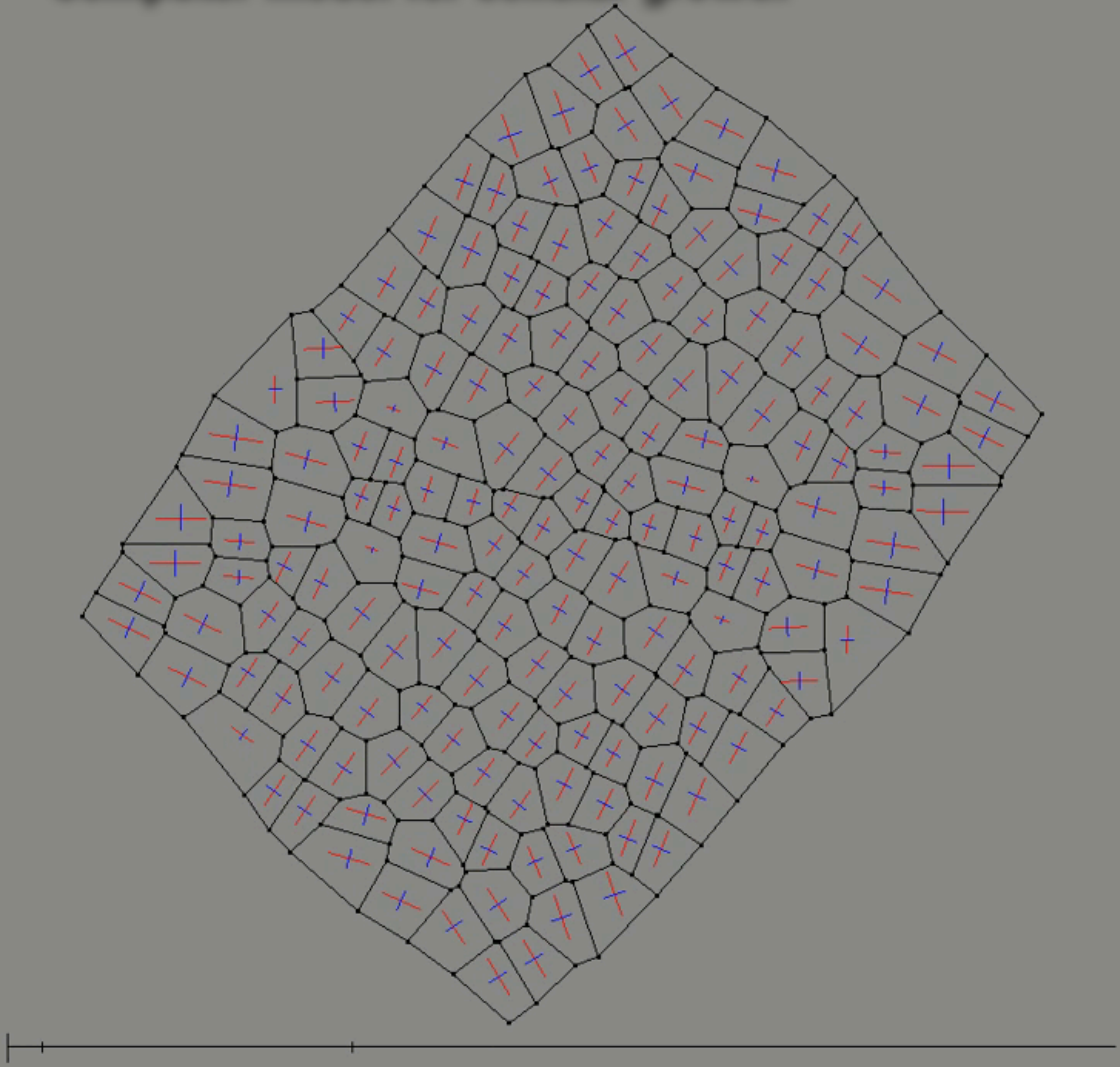


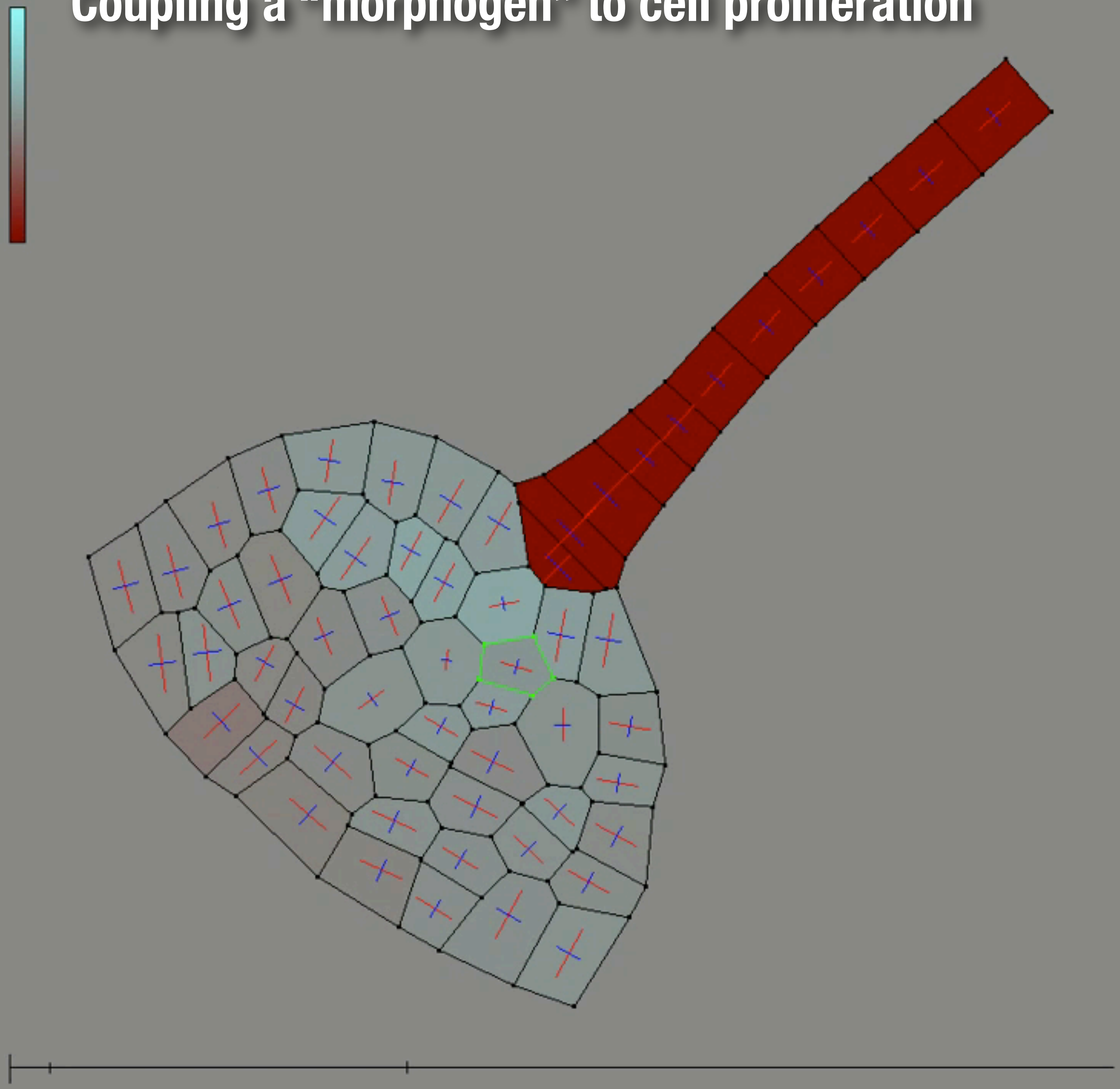
Fig. 225.

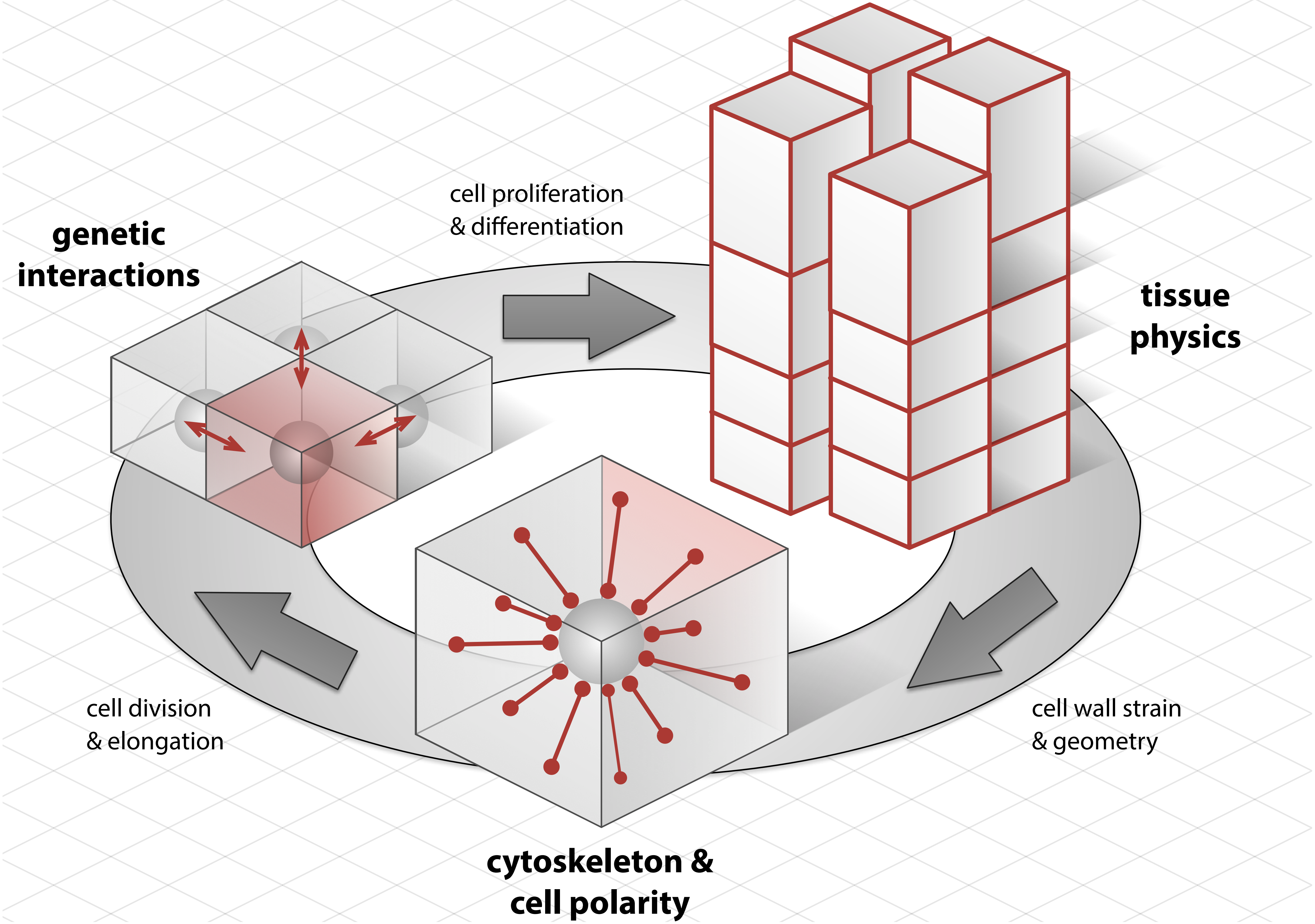


Computer model for cellular growth



Coupling a “morphogen” to cell proliferation

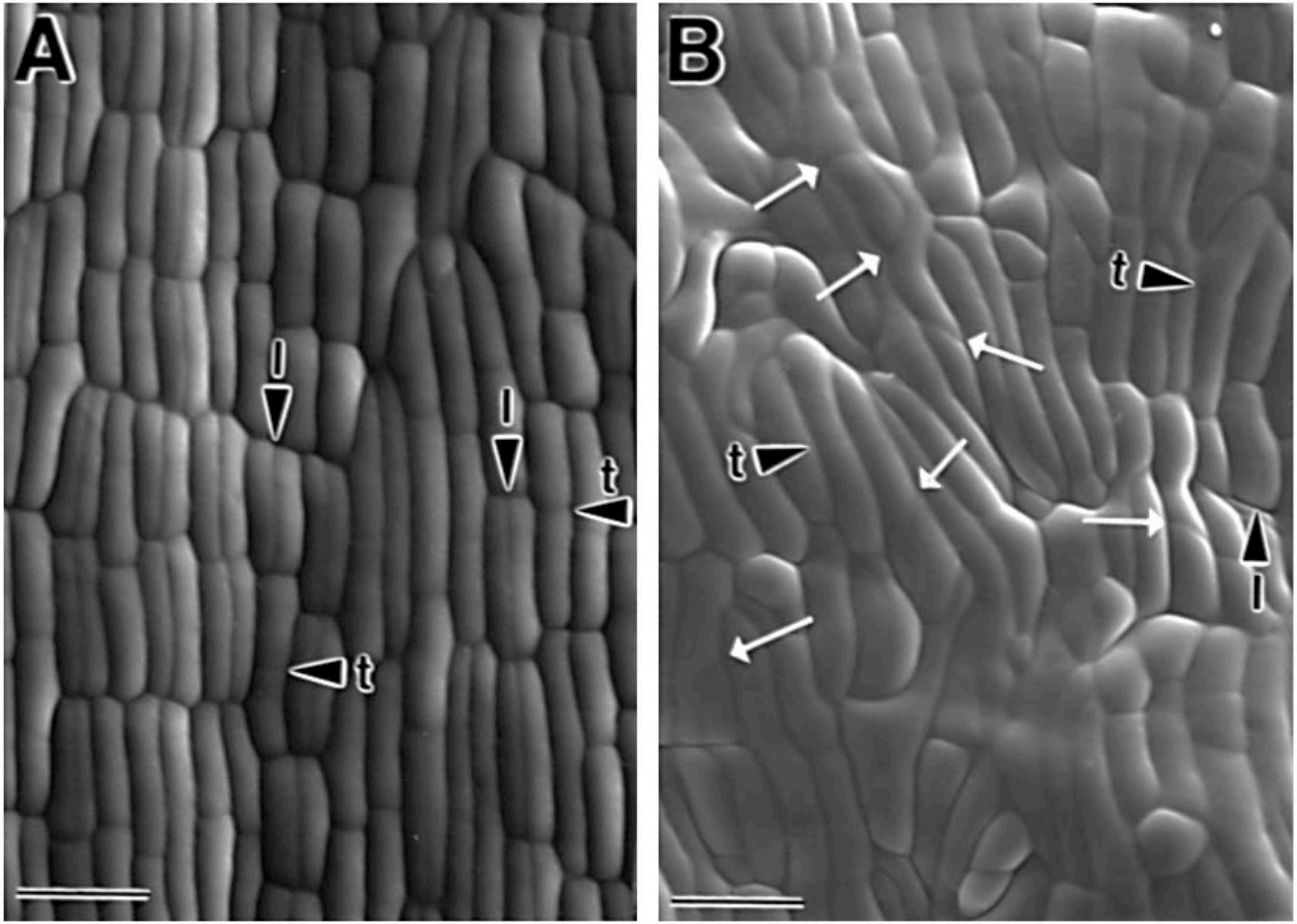


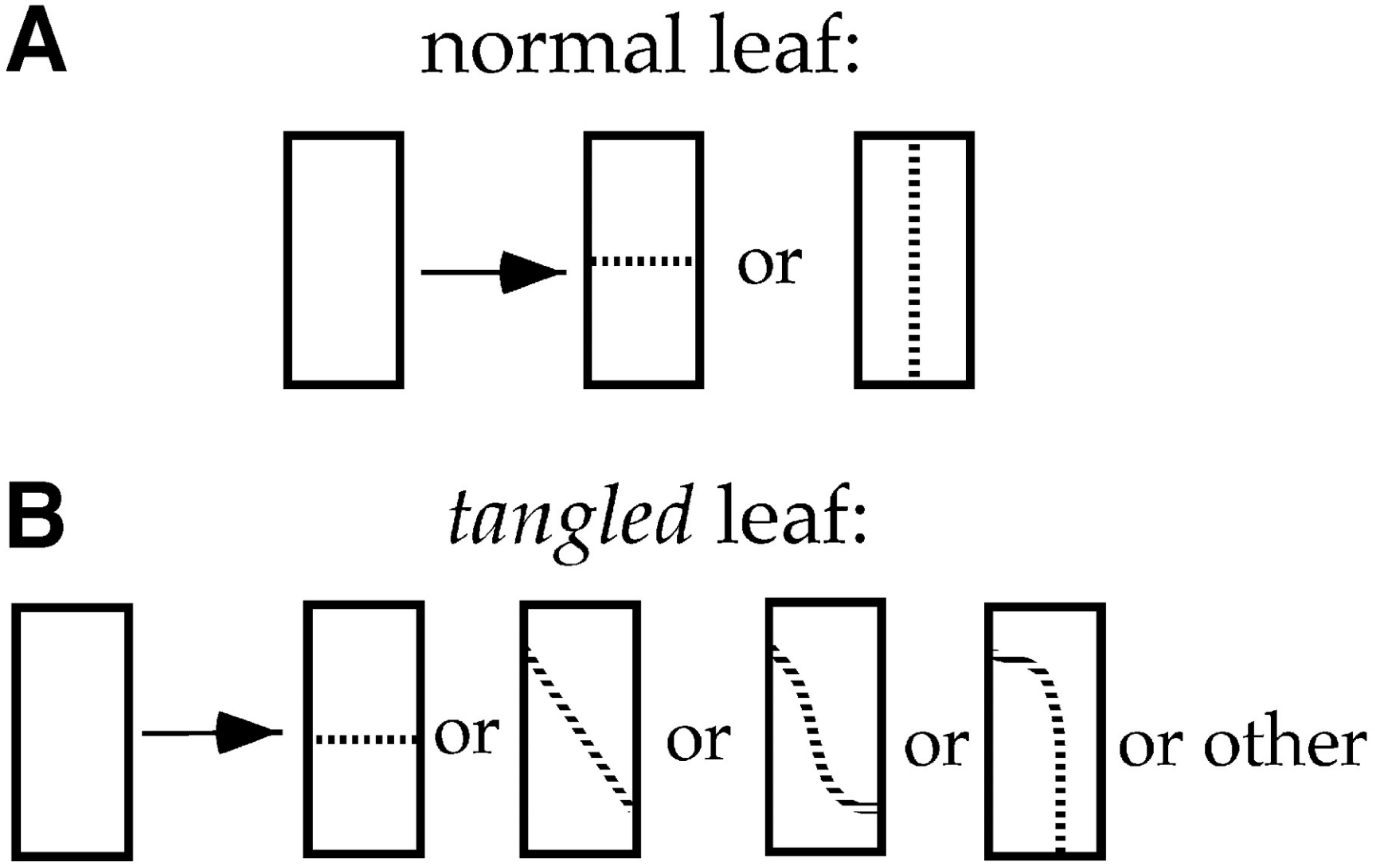


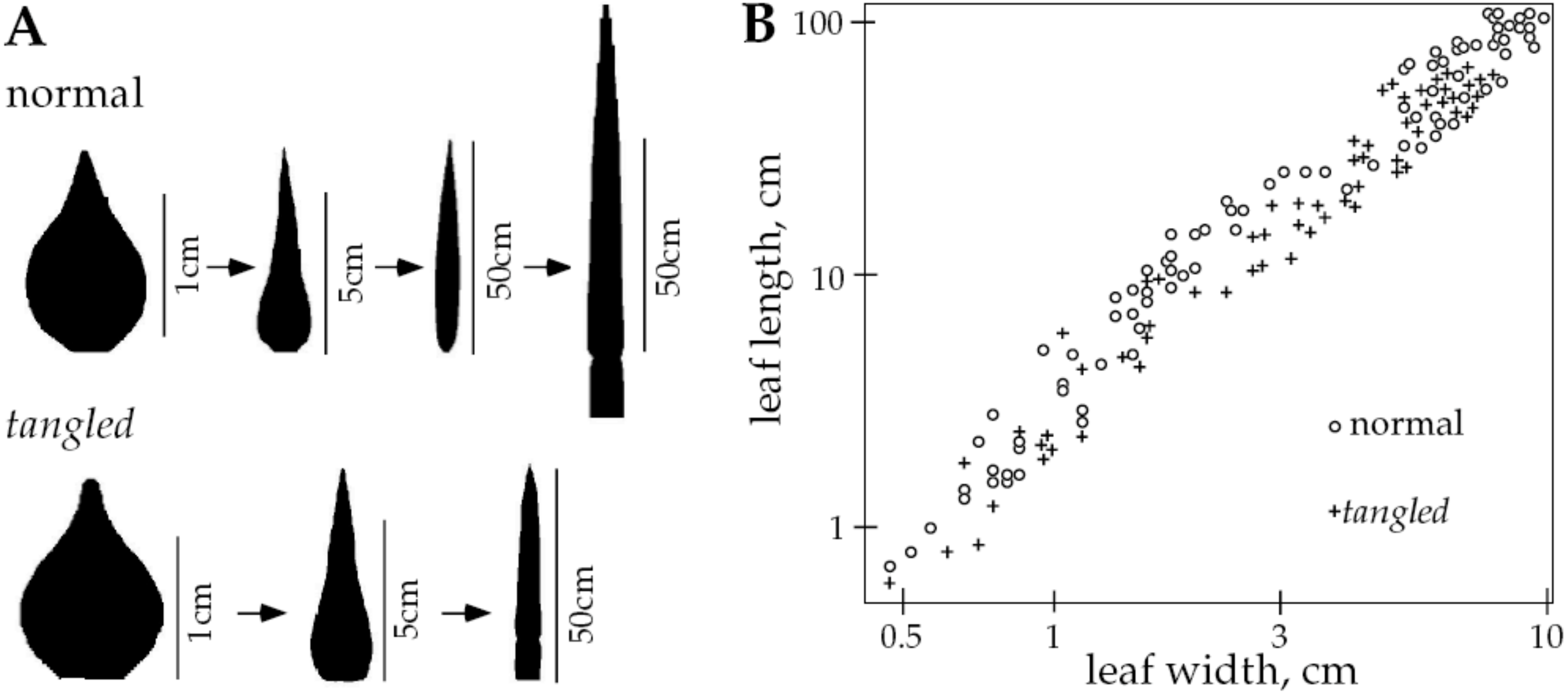
Multi-scale view of plant growth.

The tangled-1 mutation alters cell division orientations throughout maize leaf development without altering leaf shape

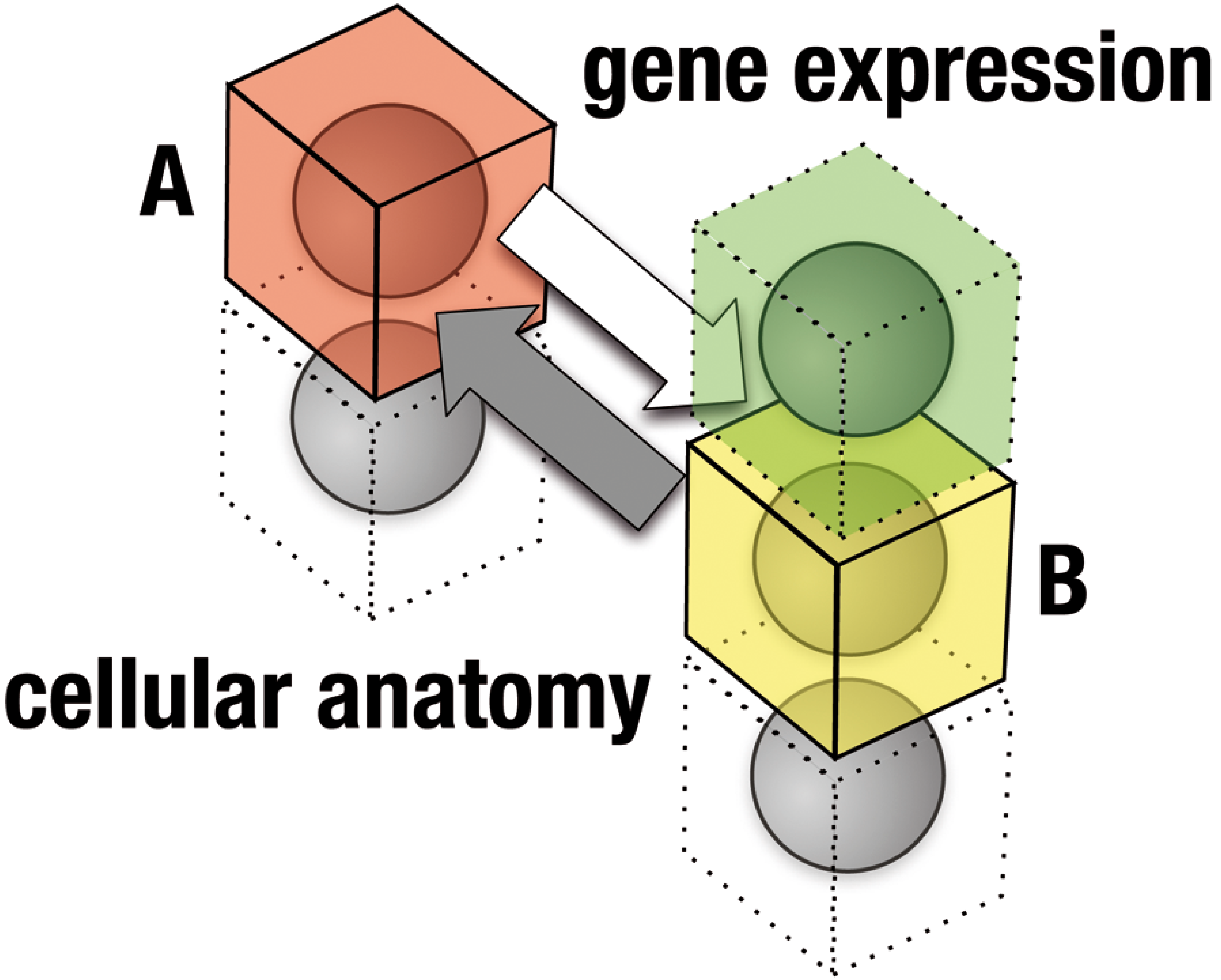
LG Smith, S Hake and AW Sylvester
Development. 122:481-9 (1996).




A
normal leaf:
or
B
tangled leaf:
or
or
or
or other


A
normal
1cm
5cm
50cm
50cm
tangled
1cm
5cm
50cm
B
100
10
1
leaf length, cm
0.5
1
3
10
leaf width, cm
○ normal
+ *tangled*

DNA modification is our tool for reprogramming agronomic characters, but many traits are morphological or physiological and scaled across whole tissues and organs. Our ability to manipulate DNA is increasing rapidly: can we reprogram large scale cellular systems for new crop traits in the future?



Are these plants related?


Cabbage

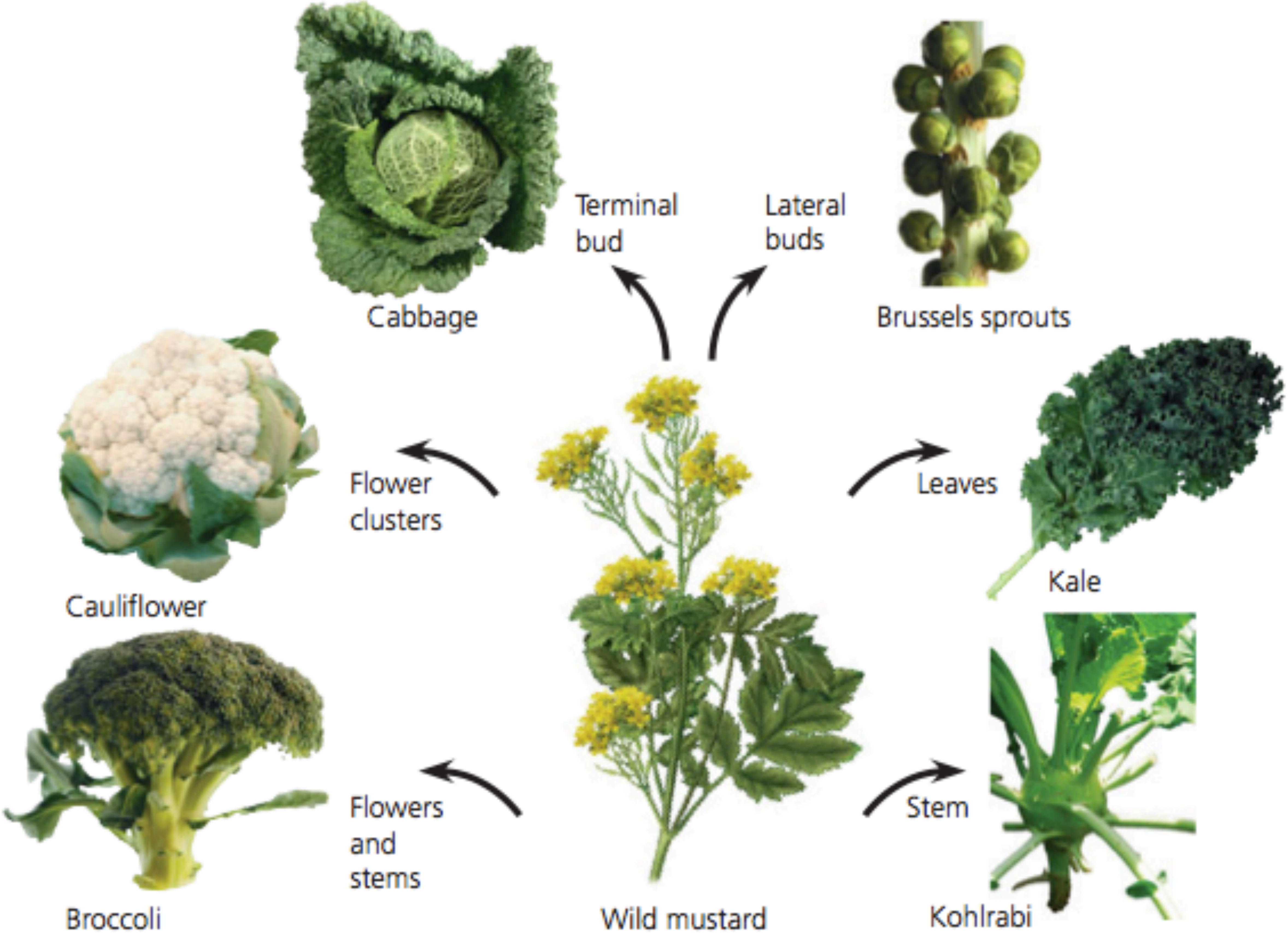

Brussels sprouts


Cauliflower


Kale


Broccoli


Kohlrabi



Crops derived from wild mustard (*Brassica oleracea*)

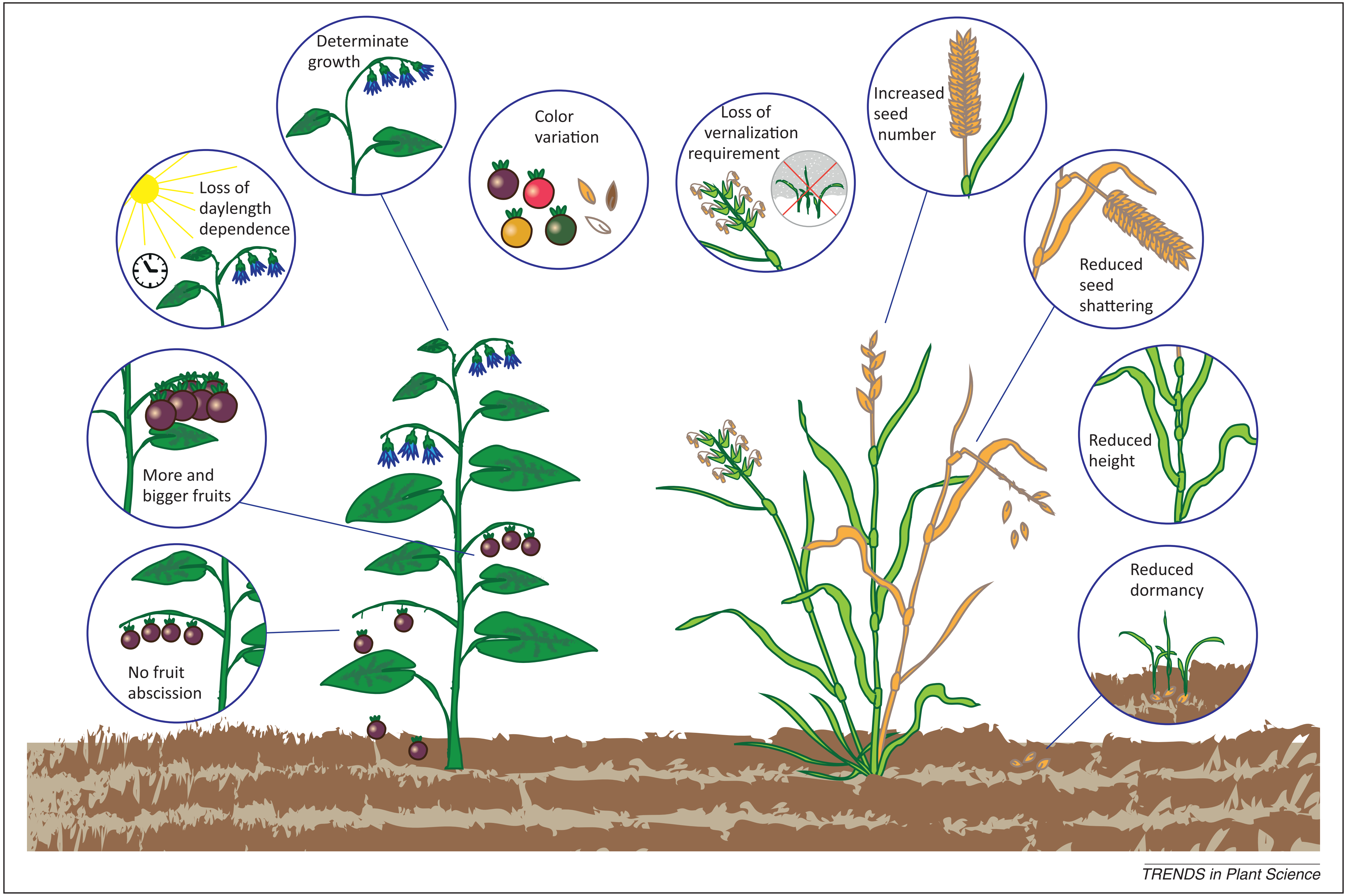
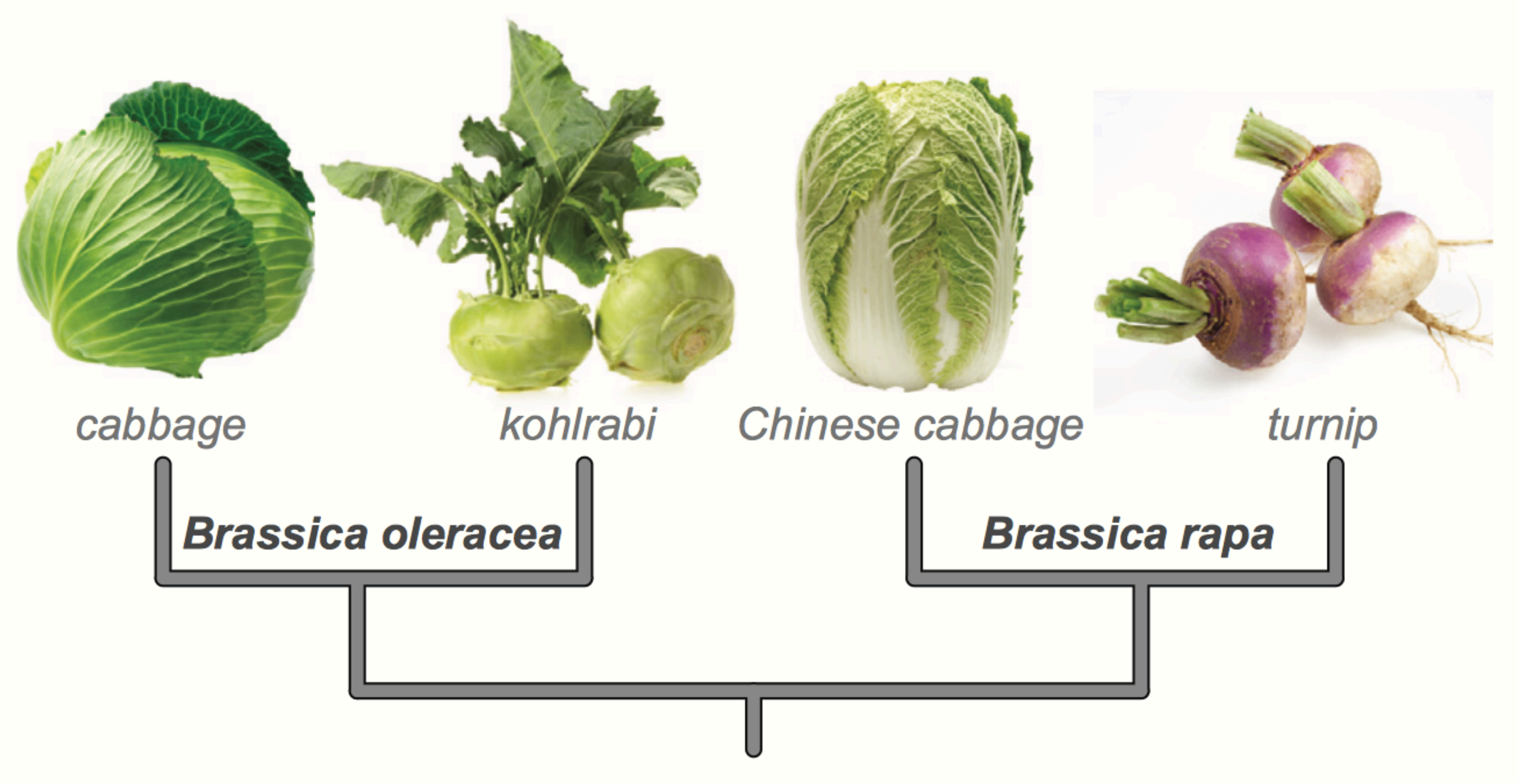
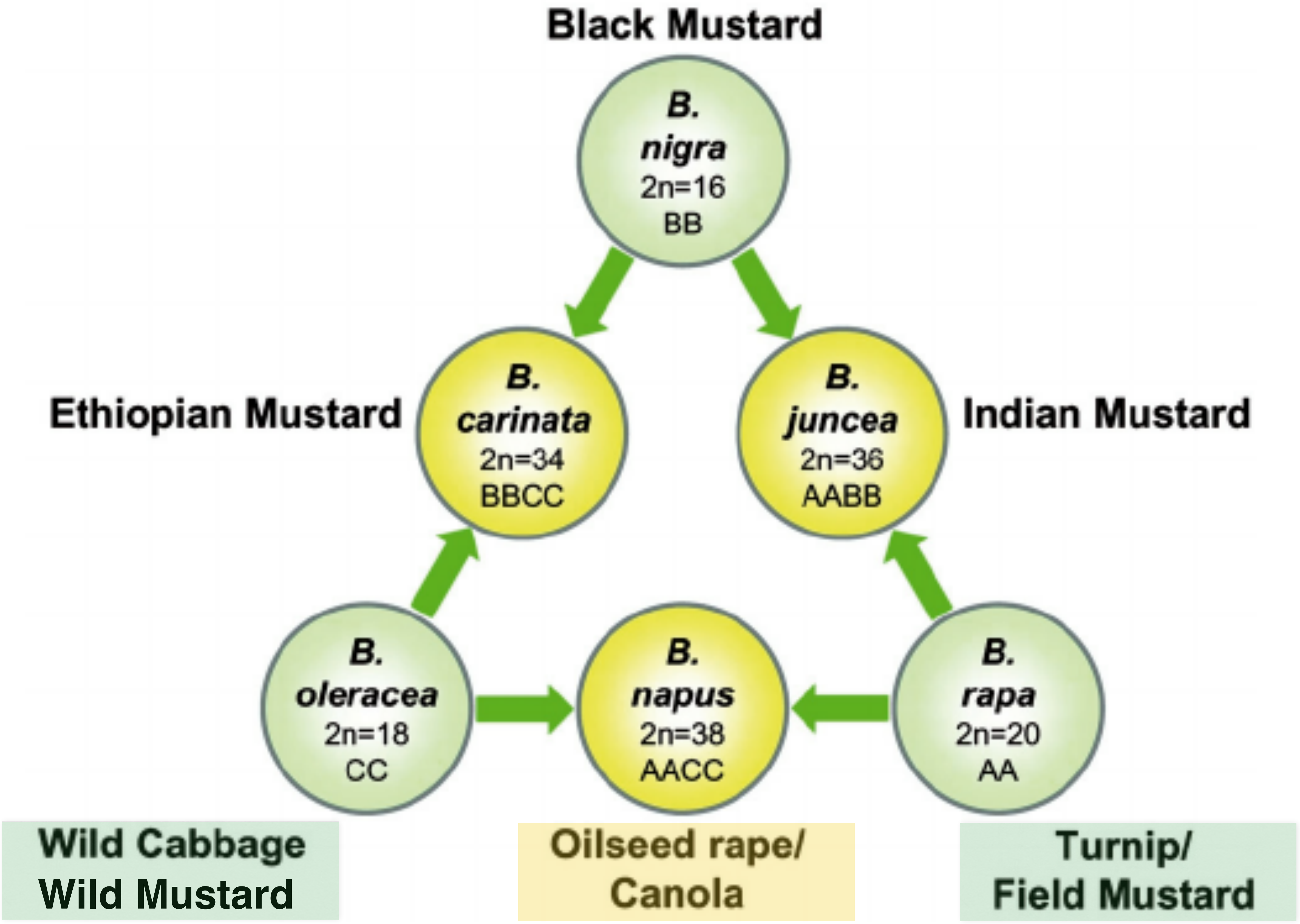


Figure 1. Convergent domestication. Convergent phenotypic changes are frequently observed in many different crops because systematic human cultivation often brings about similar demands. Attempts to maximize yield cause selective pressure for an increase in size and number of edible plant parts on the one hand and for a decrease in natural seed and fruit dispersal mechanisms to reduce yield loss on the other hand. Shifts in cultivation area often require changes in day length dependence or in the vernalization requirement and a reduction in seed dormancy is needed for synchronous germination. Small plants with a determinate growth habit are often selected because they are more robust, have a better yield to overall biomass ratio, and are better suited to mechanical harvesting methods. Finally, satisfying esthetic preferences often drives convergent adaptations, a prominent example being changes in color. Stylized examples of the major angiosperm plant lineages from which current crops originated are shown (eudicot, left; monocot, right) featuring traits of typical wild species. Characters that convergently evolved in various domesticated crops are depicted in circles.

Convergent phenotypic changes during domestication



Oilseed rape and Canola are derived from a cross between *Brassica oleracea* and *Brassica rapa*



Black Mustard

B. nigra
2n=16
BB

Ethiopian Mustard

B. carinata
2n=34
BBCC

B. juncea
2n=36
AABB

Indian Mustard

B. oleracea
2n=18
CC

B. napus
2n=38
AACC

B. rapa
2n=20
AA

Wild Cabbage
Wild Mustard

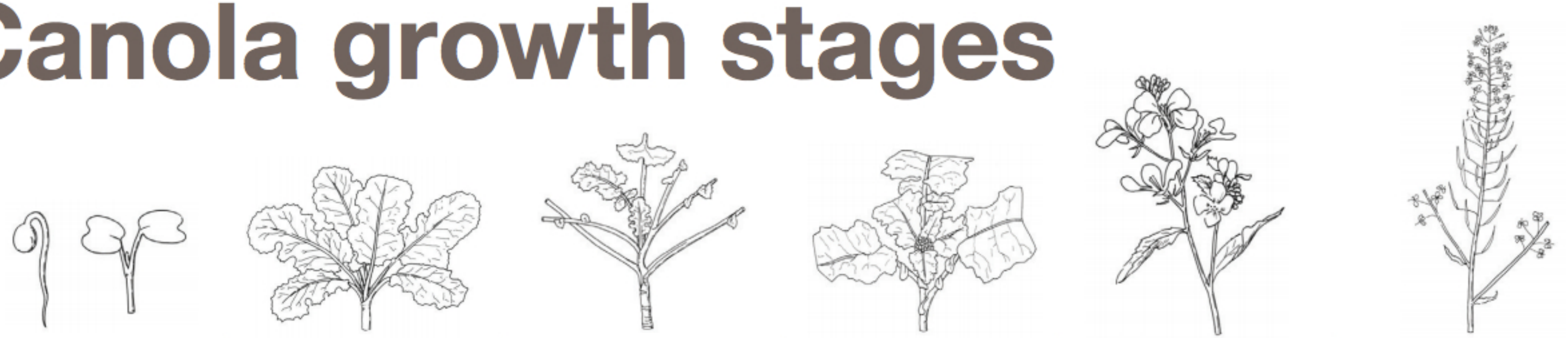
Oilseed rape/
Canola

Turnip/
Field Mustard

Brassica napus

Brassica napus seed have a 45% oil content

Canola growth stages



Stage 0 [0.0–0.8]	**Stage 1** [1.0–1.2]	**Stage 2** [2.0–2.2]	**Stage 3** [3.0–3.9]	**Stage 4** [4.1–4.9]	**Stage 5** [5.1–5.9]
Germination and emergence	Leaf production	Stem elongation	Flower bud development	Flowering	Pod development

Canola are varieties of oilseed rape (B. napus) with low erucic acid content

Crop domestication

An example of a multicellular trait: reduction of seed shatter and improved yield at harvest

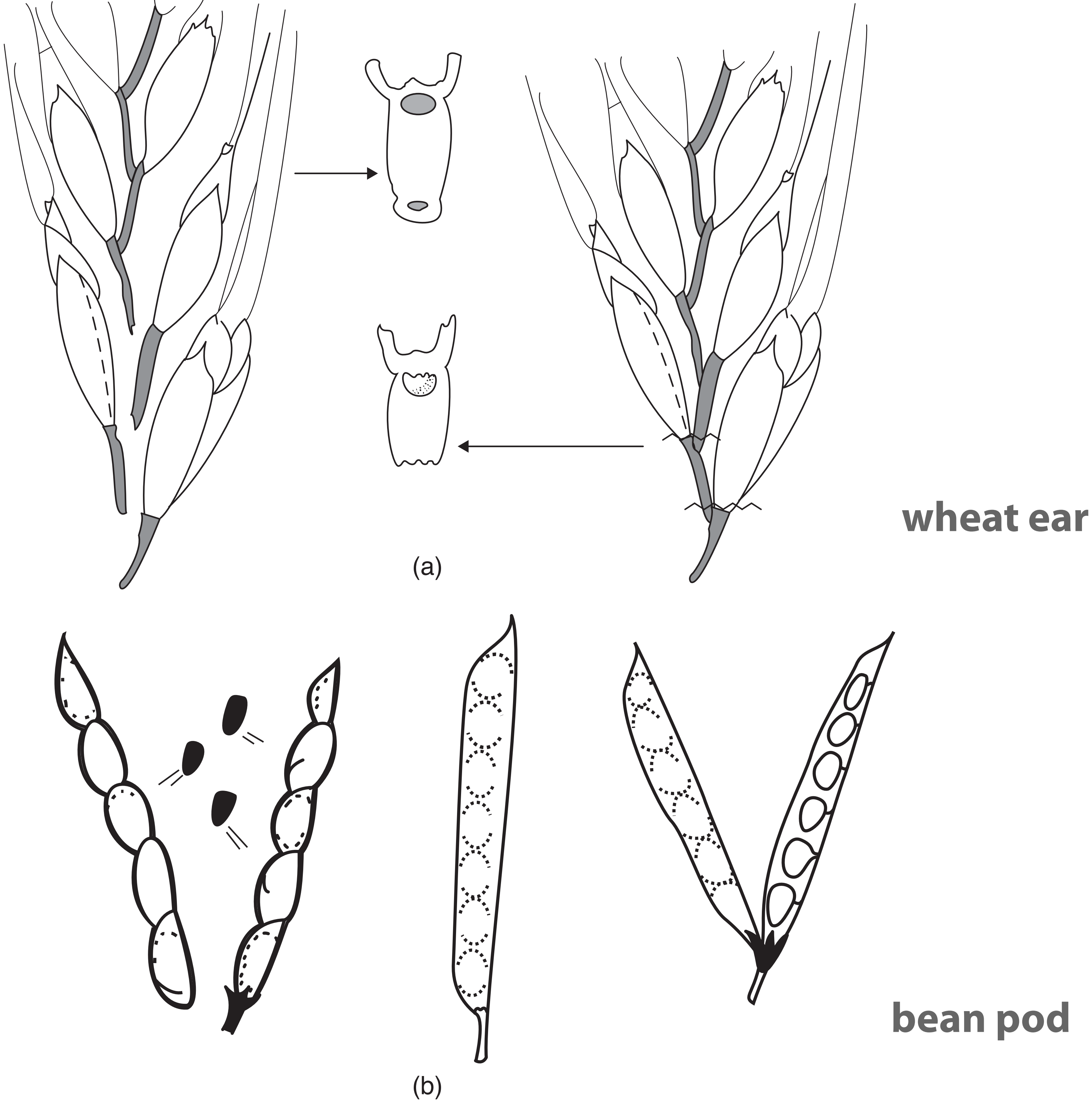
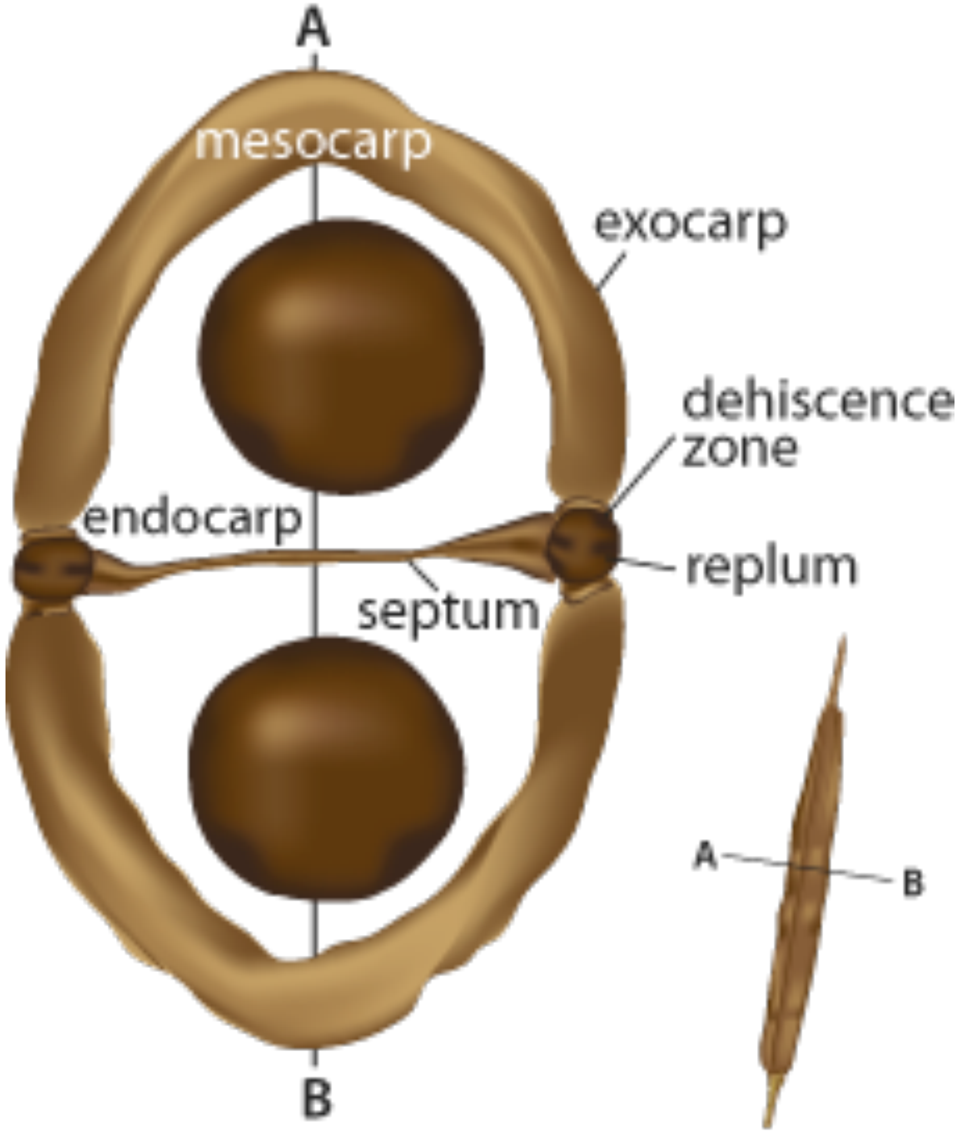
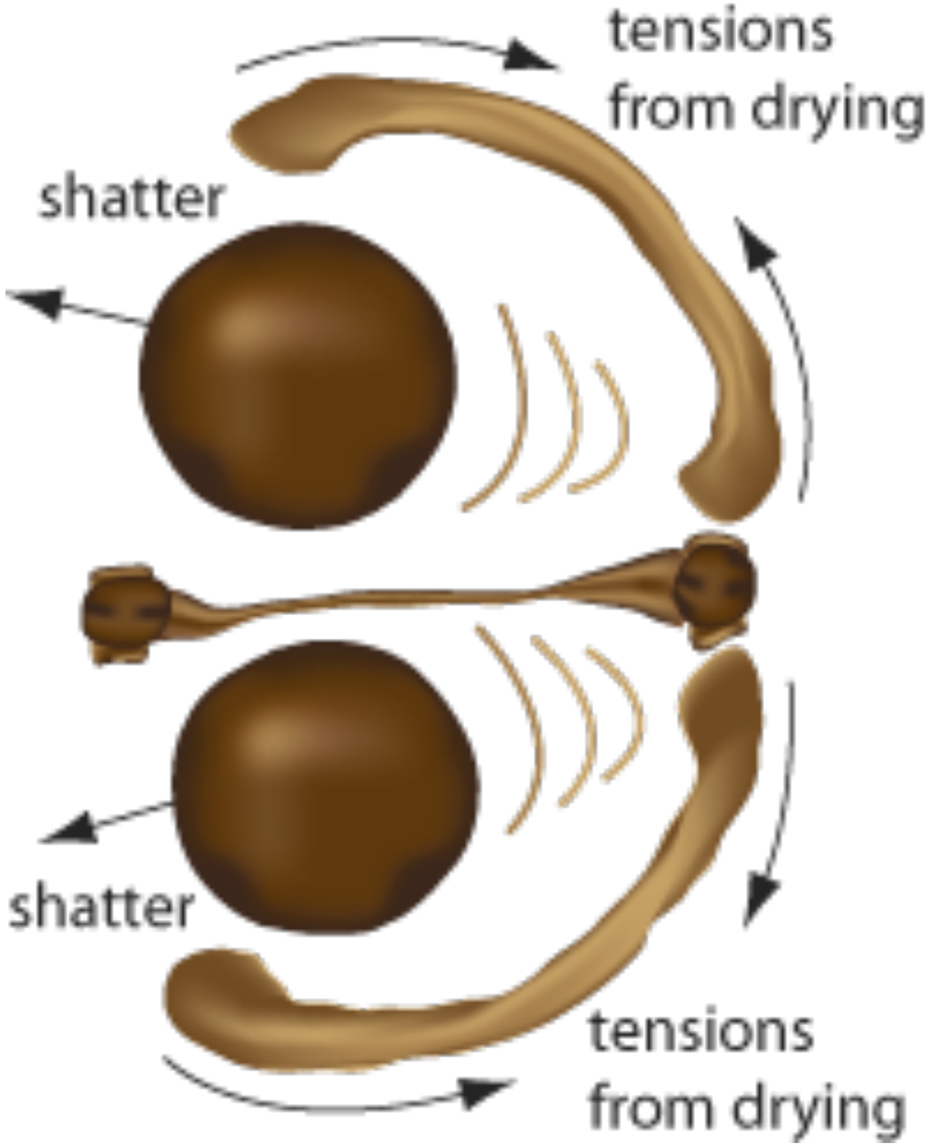


Figure 7.1 Comparisons between wild and domesticated plants in terms of seed dispersal. (a) Comparison between a wild shattering wheat ear (left) and domestic wheat ear with a tough rachis, which requires pounding to break apart (right). The form of rachis segments that can be recovered archaeologically is shown in the middle. (b) Generalized wild bean with pod that twists and opens, dispersing seeds (left) compared with a domestic pod that remains closed (middle) and must be split open by human force (right).

Pod Shatter can result in substantial losses of yield (25-50%)





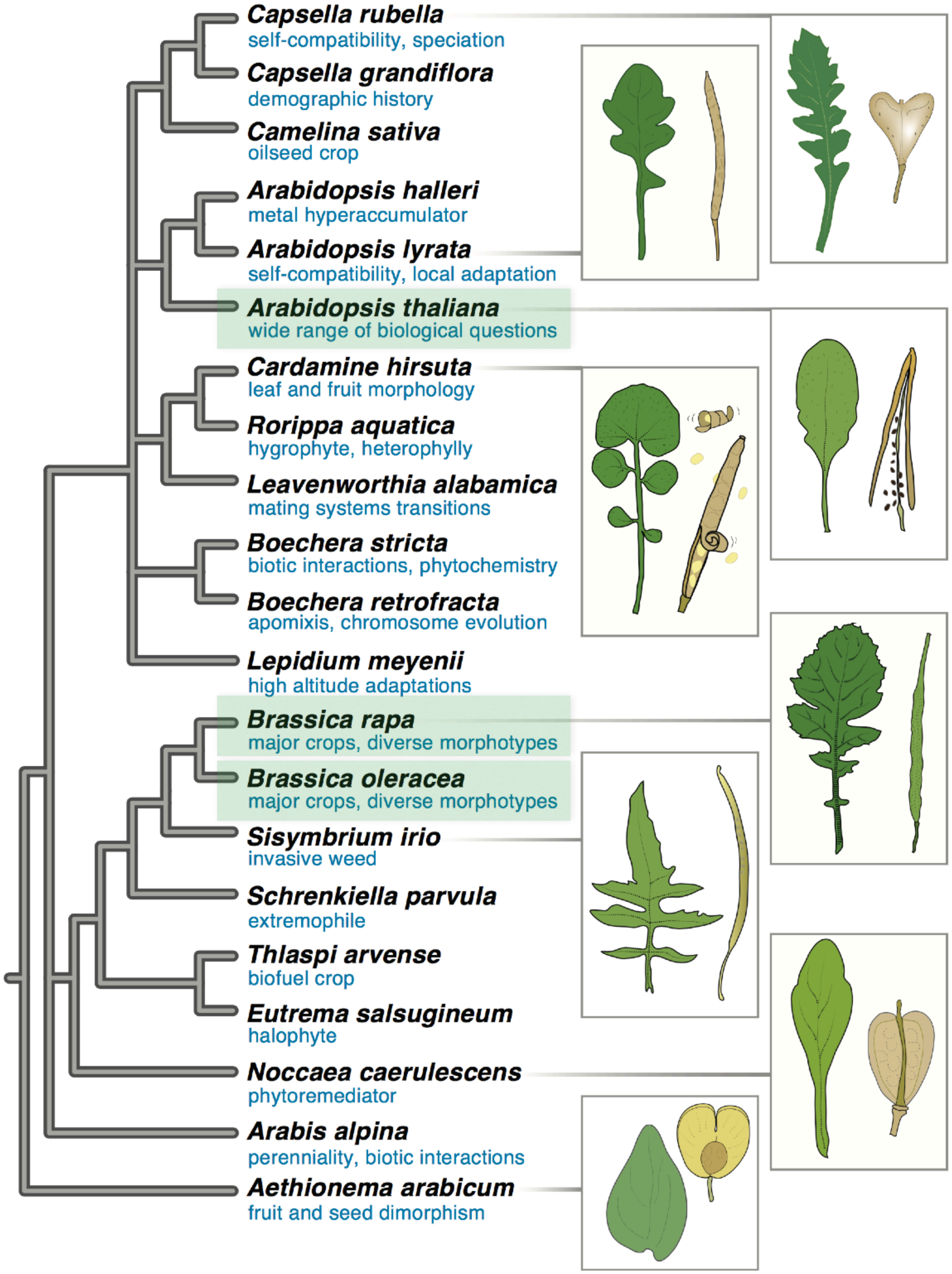
Pod Shatter at harvest of *Brassica rapa* (rapeseed)

Seed pods are often fragile in the weeks leading up to harvest. During this stage seed pods go through a process of dehiscence (splitting open), commonly known as pod shatter.
This process can result in:

- substantial seed loss (up to 25%)
- decrease in yield;
- greater number of volunteers in next season's crop.

In adverse conditions prior to harvest the potential loss can be as high as 50%

Brassica species are closely related to the model plant Arabidopsis.



Capsella rubella
self-compatibility, speciation

Capsella grandiflora
demographic history

Camelina sativa
oilseed crop

Arabidopsis halleri
metal hyperaccumulator

Arabidopsis lyrata
self-compatibility, local adaptation

Arabidopsis thaliana
wide range of biological questions

Cardamine hirsuta
leaf and fruit morphology

Rorippa aquatica
hygrophyte, heterophylly

Leavenworthia alabamica
mating systems transitions

Boechera stricta
biotic interactions, phytochemistry

Boechera retrofracta
apomixis, chromosome evolution

Lepidium meyenii
high altitude adaptations

Brassica rapa
major crops, diverse morphotypes

Brassica oleracea
major crops, diverse morphotypes

Sisymbrium irio
invasive weed

Schrenkiella parvula
extremophile

Thlaspi arvense
biofuel crop

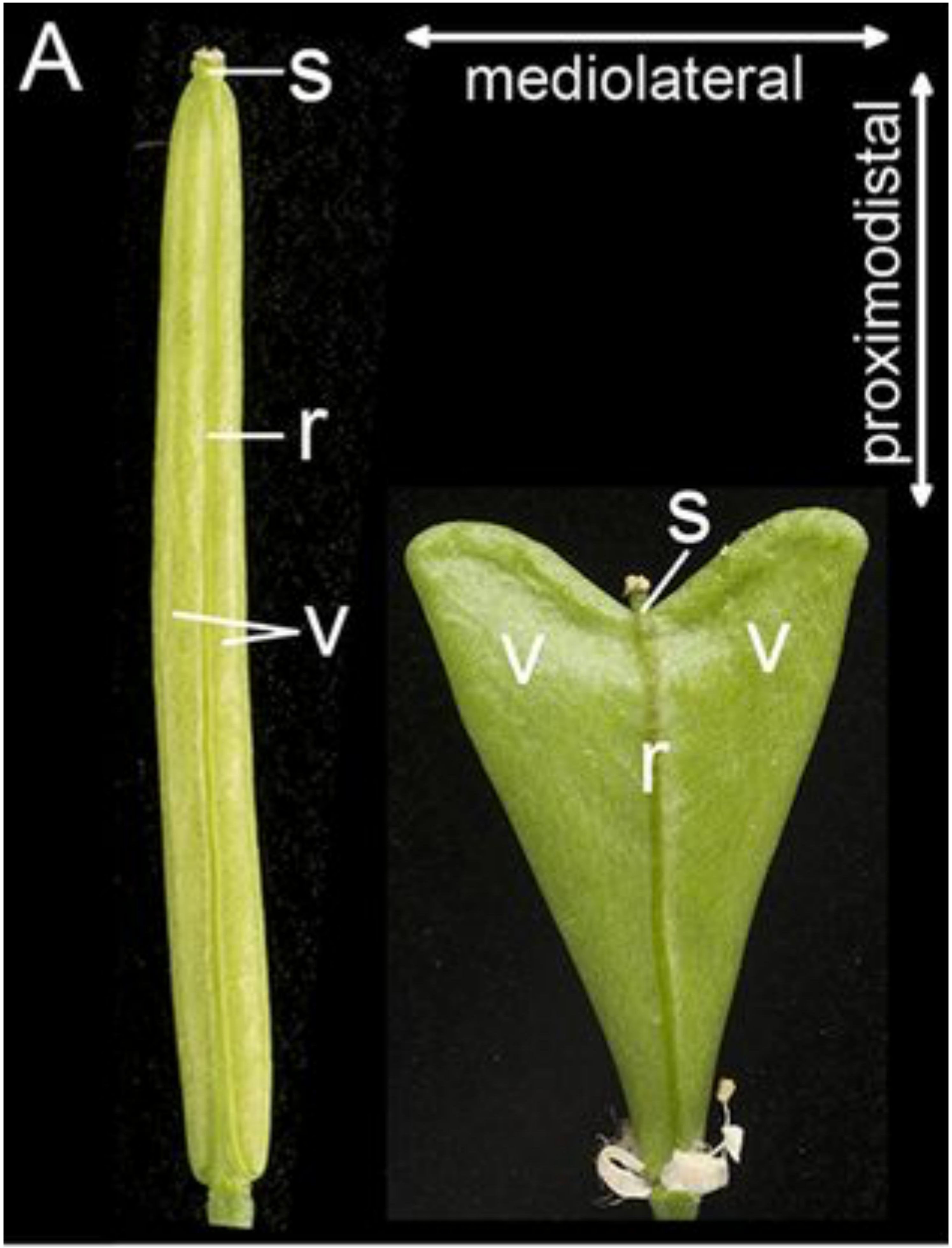
Eutrema salsugineum
halophyte

Noccaea caerulescens
phytoremediator

Arabis alpina
perenniality, biotic interactions

Aethionema arabicum
fruit and seed dimorphism

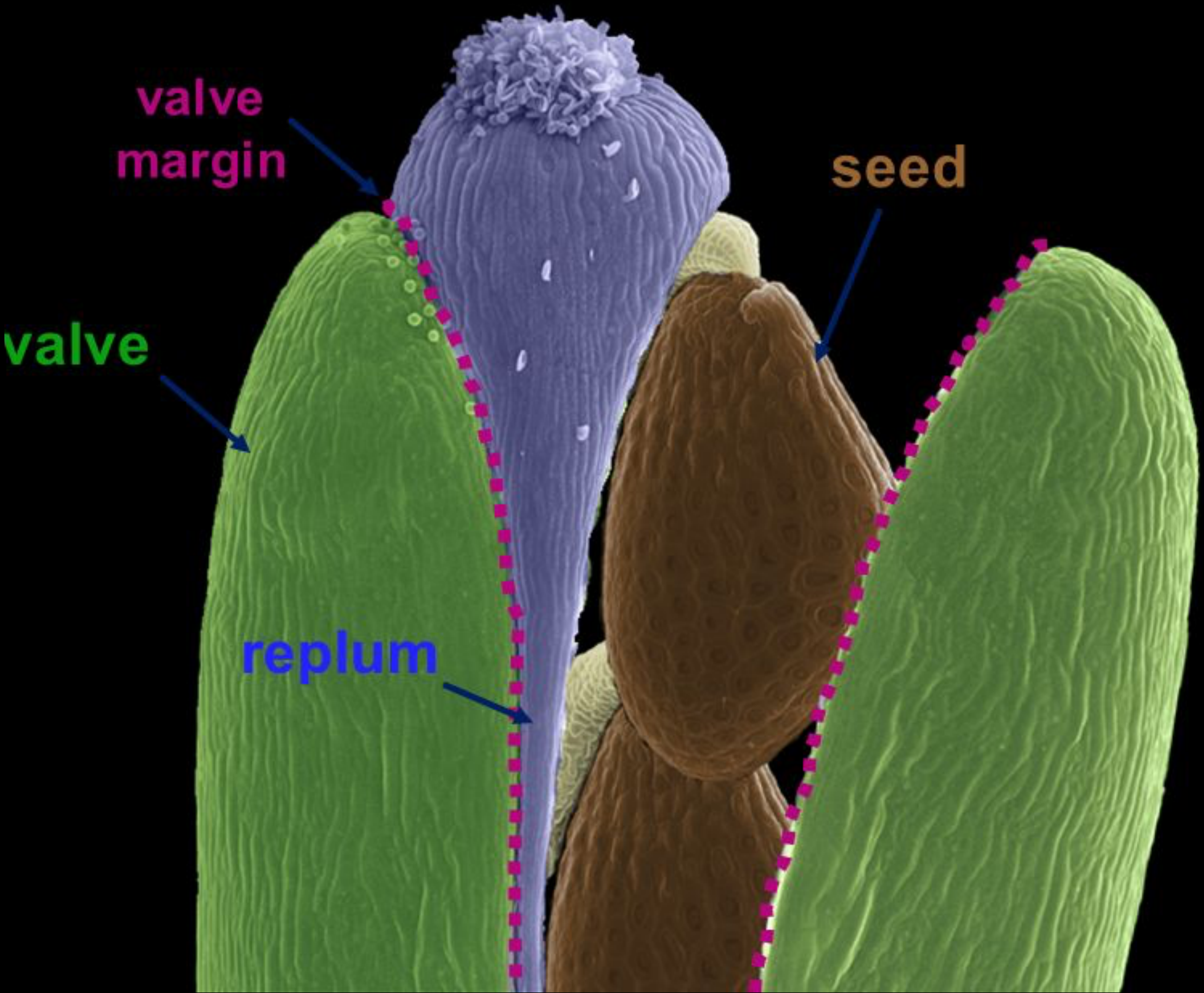
Current Opinion in Plant Biology



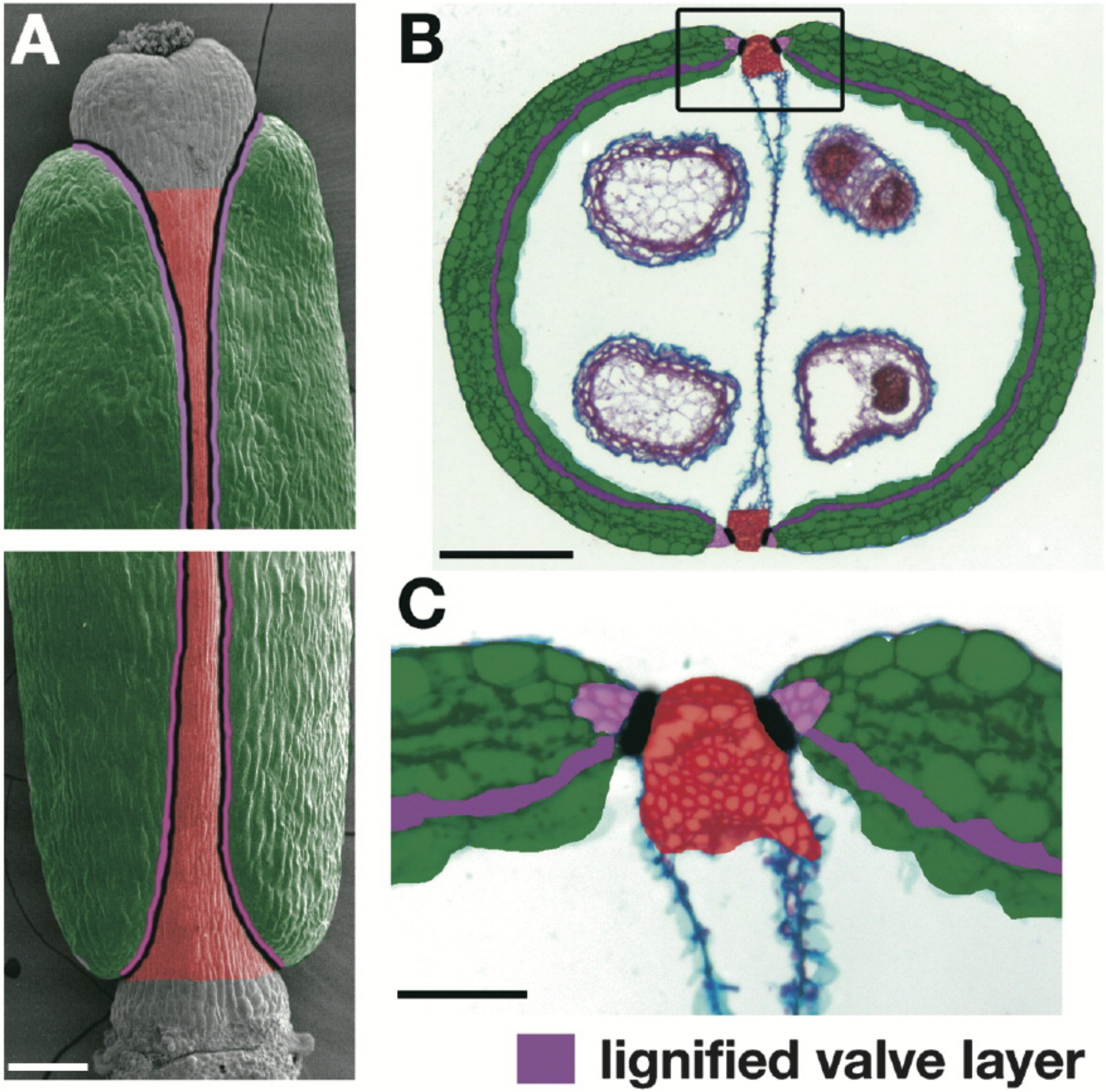
Arabidopsis also bears its seed in siliques (seed pods) which are anatomically similar to those of rapeseed plants.

left: ***Arabidopsis thaliana***
right: ***Capsella rubella***
(V=valve, r=replum, S= stigma)

Arabidopsis fruit opening

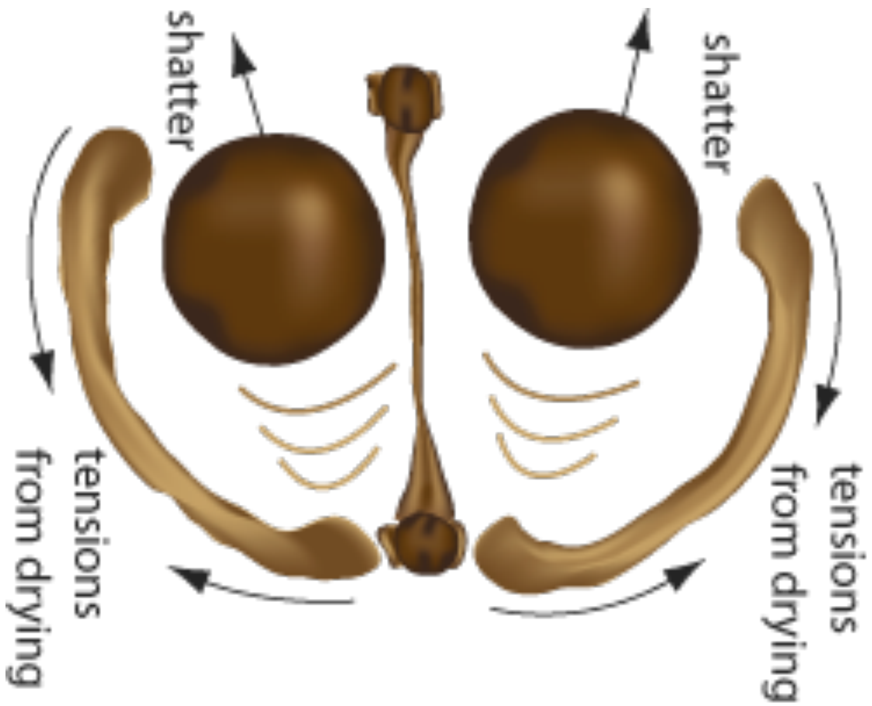


Specialised cells and valve dehiscence in Arabidopsis

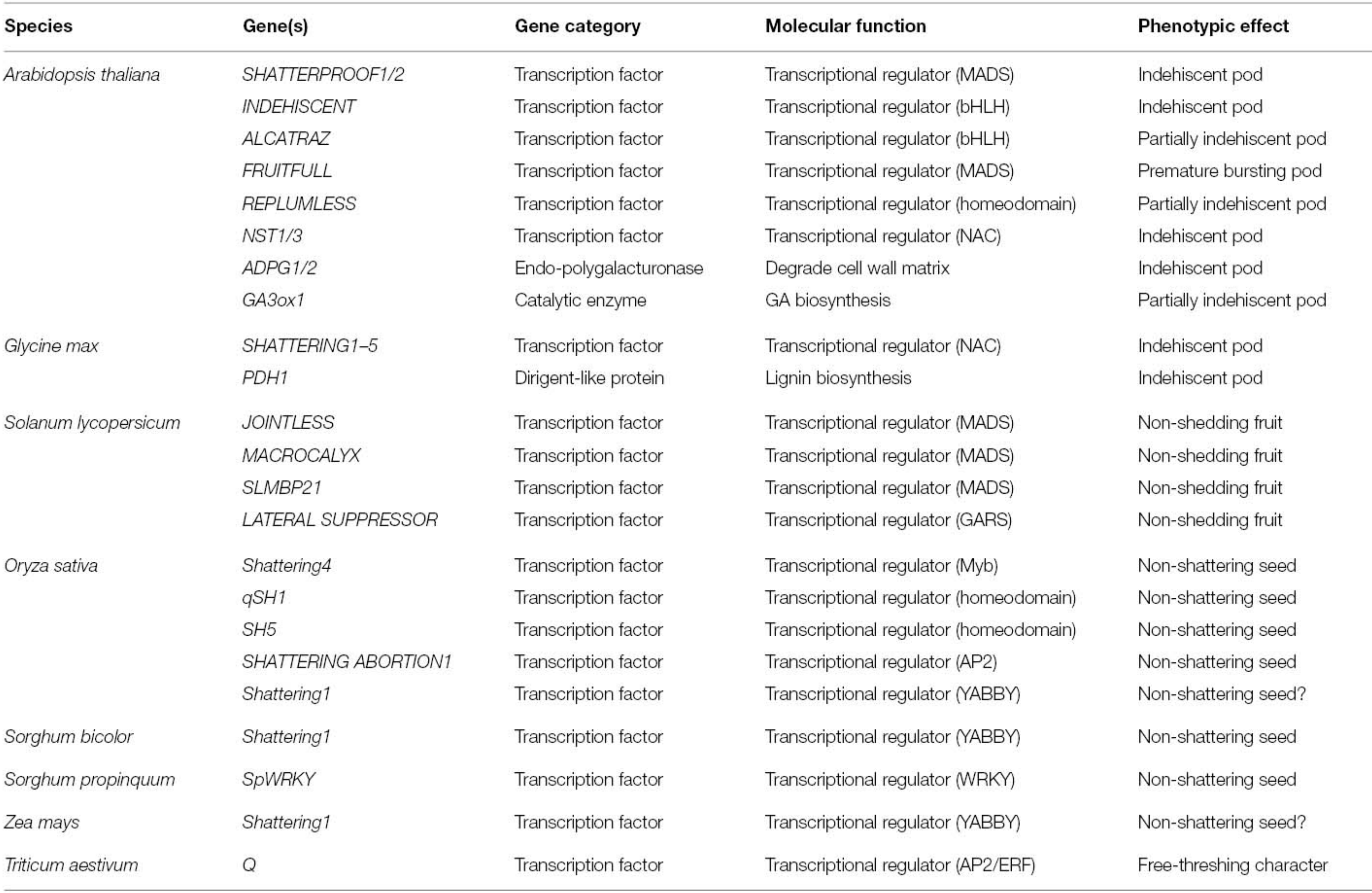


🟩 valve
🟥 replum

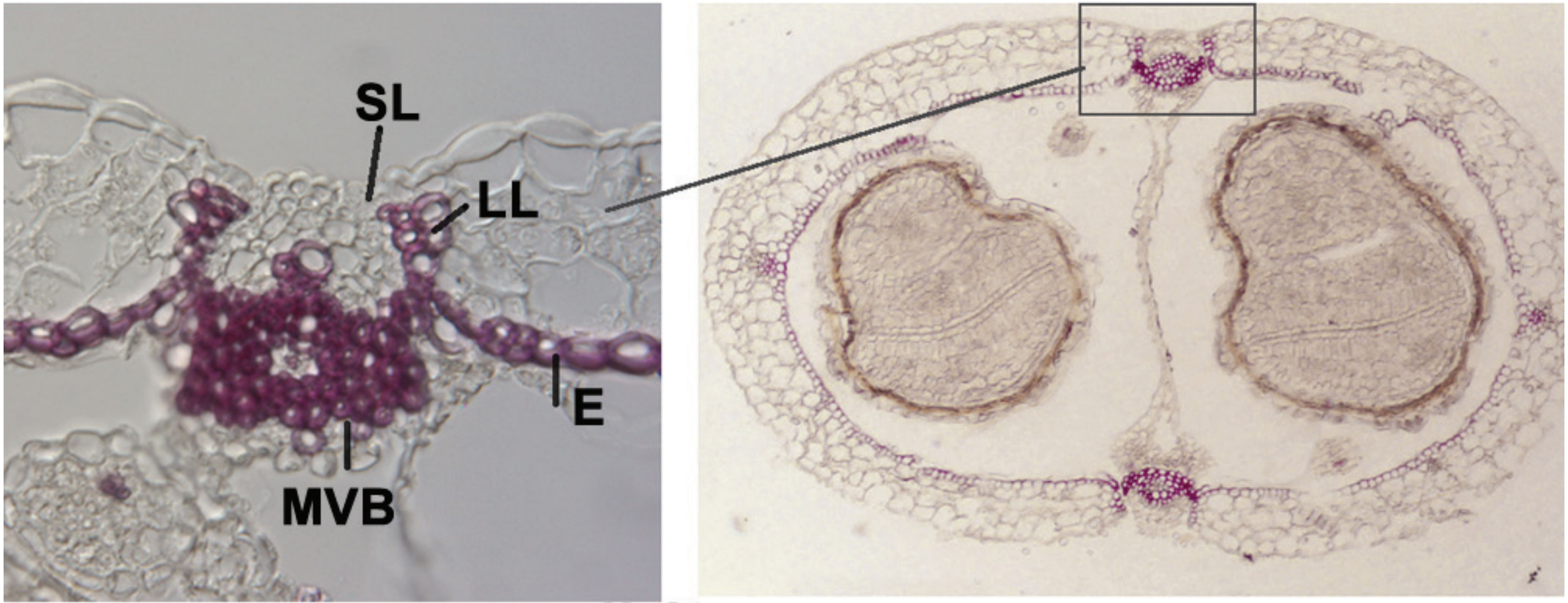
🟪 lignified valve layer
🟪 lignified margin layer
⬛ separation layer



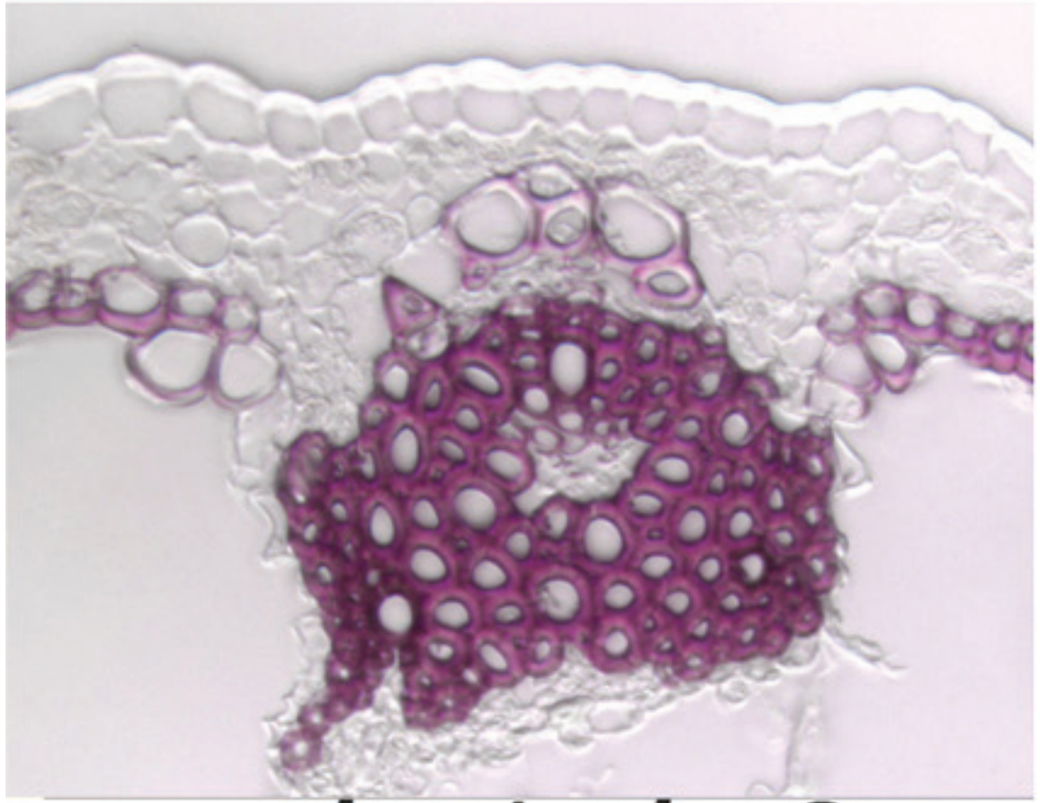
Genetically identified regulators of seed shatter



Species	Gene(s)	Gene category	Molecular function	Phenotypic effect
Arabidopsis thaliana	*SHATTERPROOF1/2*	Transcription factor	Transcriptional regulator (MADS)	Indehiscent pod
	INDEHISCENT	Transcription factor	Transcriptional regulator (bHLH)	Indehiscent pod
	ALCATRAZ	Transcription factor	Transcriptional regulator (bHLH)	Partially indehiscent pod
	FRUITFULL	Transcription factor	Transcriptional regulator (MADS)	Premature bursting pod
	REPLUMLESS	Transcription factor	Transcriptional regulator (homeodomain)	Partially indehiscent pod
	NST1/3	Transcription factor	Transcriptional regulator (NAC)	Indehiscent pod
	ADPG1/2	Endo-polygalacturonase	Degrade cell wall matrix	Indehiscent pod
	GA3ox1	Catalytic enzyme	GA biosynthesis	Partially indehiscent pod
Glycine max	*SHATTERING1–5*	Transcription factor	Transcriptional regulator (NAC)	Indehiscent pod
	PDH1	Dirigent-like protein	Lignin biosynthesis	Indehiscent pod
Solanum lycopersicum	*JOINTLESS*	Transcription factor	Transcriptional regulator (MADS)	Non-shedding fruit
	MACROCALYX	Transcription factor	Transcriptional regulator (MADS)	Non-shedding fruit
	SLMBP21	Transcription factor	Transcriptional regulator (MADS)	Non-shedding fruit
	LATERAL SUPPRESSOR	Transcription factor	Transcriptional regulator (GARS)	Non-shedding fruit
Oryza sativa	*Shattering4*	Transcription factor	Transcriptional regulator (Myb)	Non-shattering seed
	qSH1	Transcription factor	Transcriptional regulator (homeodomain)	Non-shattering seed
	SH5	Transcription factor	Transcriptional regulator (homeodomain)	Non-shattering seed
	SHATTERING ABORTION1	Transcription factor	Transcriptional regulator (AP2)	Non-shattering seed
	Shattering1	Transcription factor	Transcriptional regulator (YABBY)	Non-shattering seed?
Sorghum bicolor	*Shattering1*	Transcription factor	Transcriptional regulator (YABBY)	Non-shattering seed
Sorghum propinquum	*SpWRKY*	Transcription factor	Transcriptional regulator (WRKY)	Non-shattering seed
Zea mays	*Shattering1*	Transcription factor	Transcriptional regulator (YABBY)	Non-shattering seed?
Triticum aestivum	*Q*	Transcription factor	Transcriptional regulator (AP2/ERF)	Free-threshing character



wildtype



shp1 shp2

Mutation of *shatterproof1* and *shatterproof2* results in loss of the lignified layer (LL) and separation layer(SL) within the dehiscence zone, and produces a shatterproof silique.

SHATTERPROOF (*SHP*) expression pattern

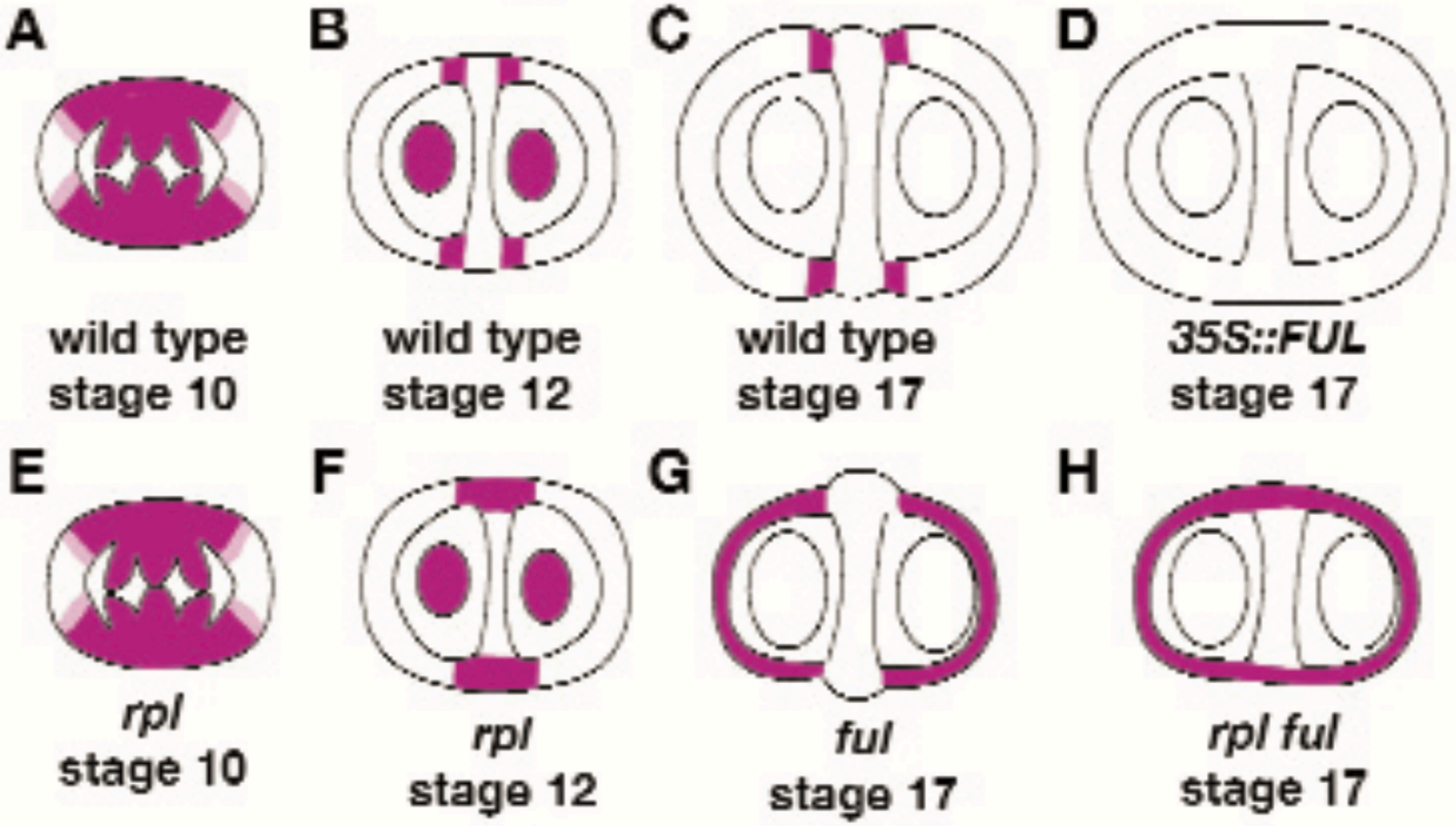
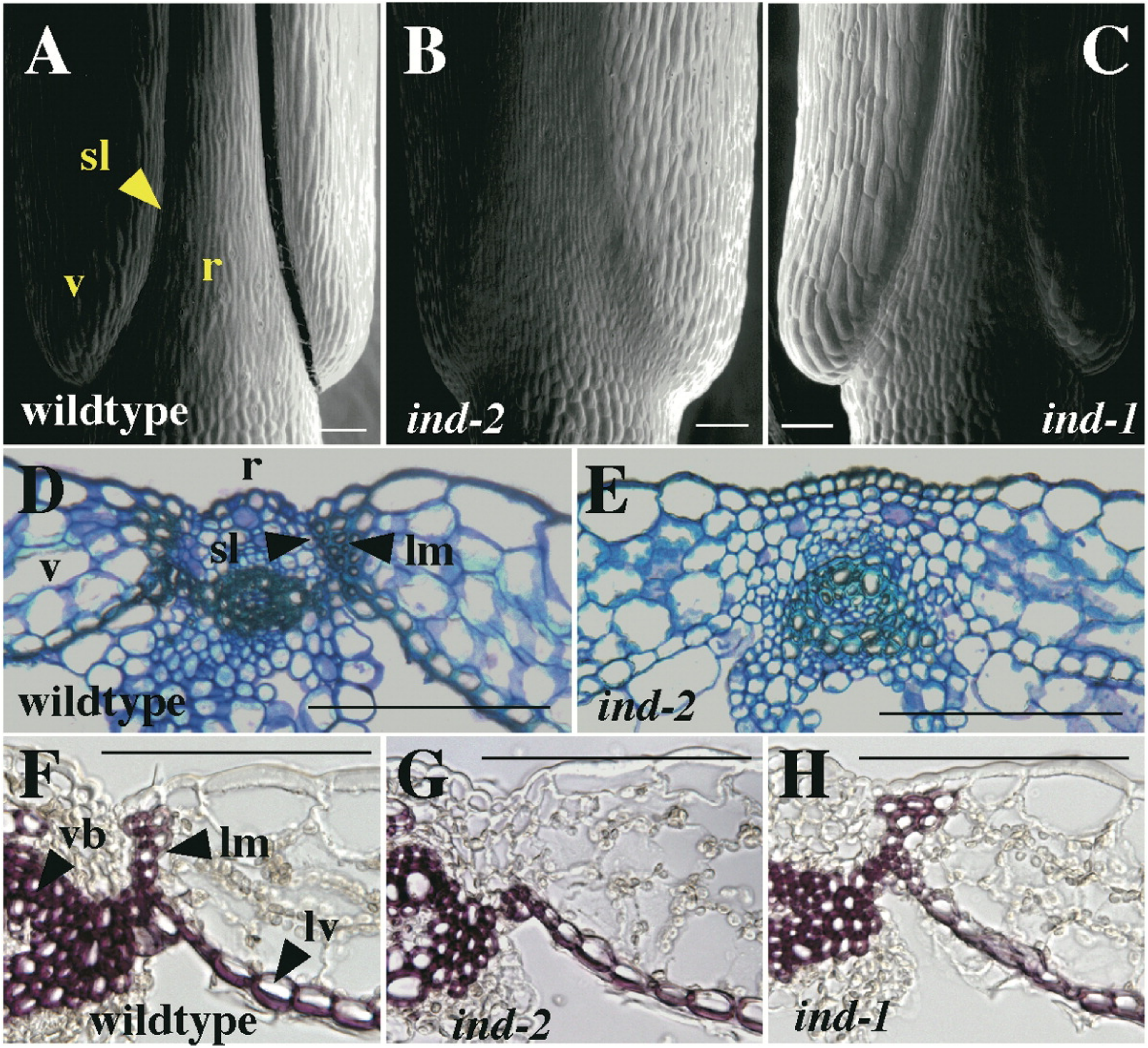
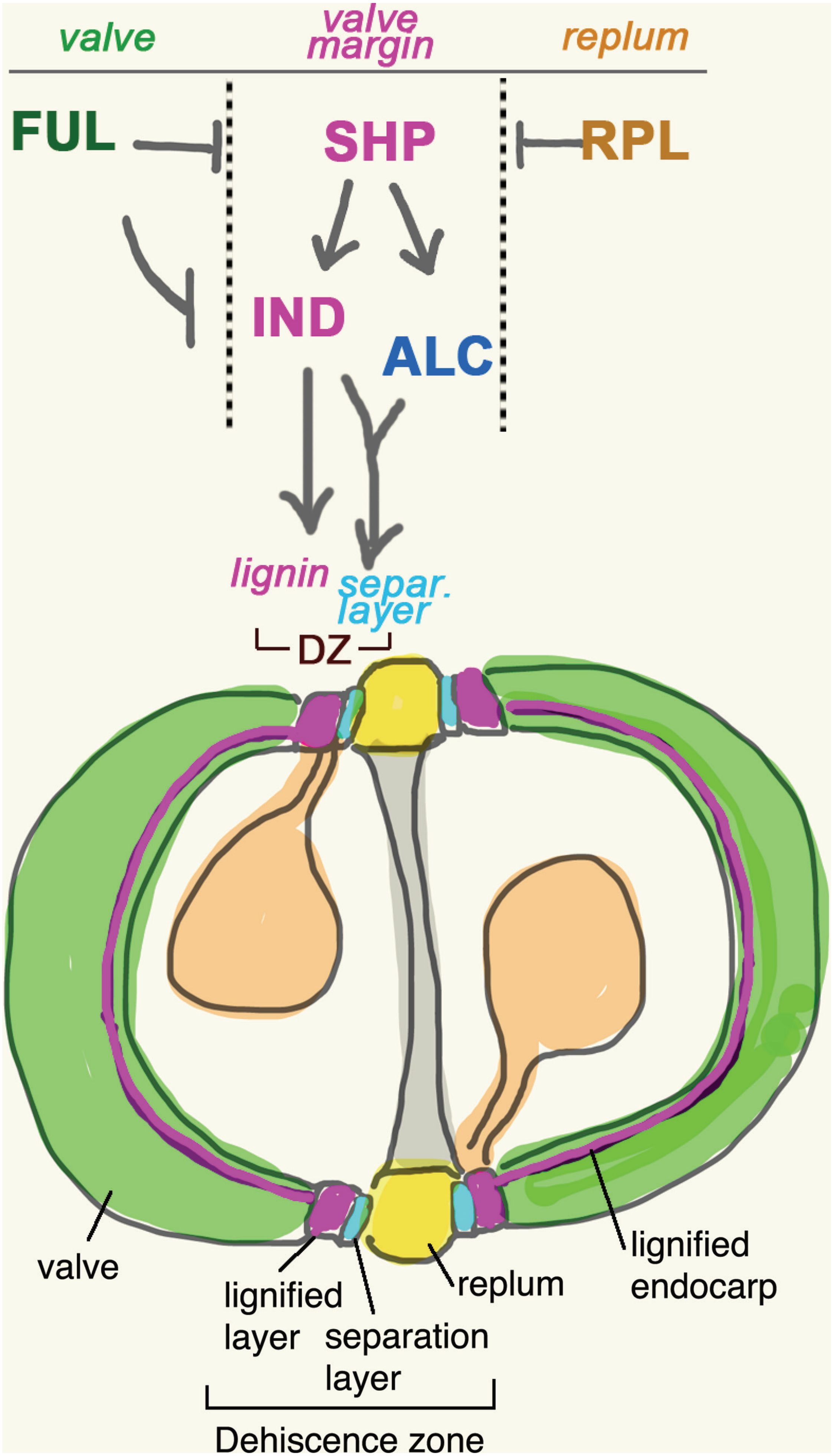


Figure 15. *SHP* expression is negatively regulated by *FUL* and *RPL.* (A) Early in development the *SHP* genes are broadly expressed in the gynoecium. At stage 10, their expression extends throughout the valve margins, replum, septum, and developing ovules. Weak expression is also seen extending into the edges of the valves. (B) At stage 12, *SHP* expression is limited specifically to the valve margins. *SHP* also continues to be expressed in the developing ovules. (C) *SHP* continues to be expressed in the valve margins through stage 17. (D) Ectopic expression of *FUL* in *35S::FUL* fruit is sufficient to block expression of *SHP* in the valve margins. (E) In *rpl* mutants, *SHP* expression is similar to wild type in early stages. (F) At stage 12 in *rpl* mutants, *SHP* continues to be expressed in the replum indicating that *RPL* is required to negatively regulate *SHP* expression in the replum. *SHP* is ectopically expressed in the replum region of *rpl* mutants through stage 17 (not shown). (G) In *ful* mutants, *SHP* is ectopically expressed throughout the valves indicating that *FUL* is required to negatively regulate *SHP* expression in the valves. (H) In *rpl ful* double mutants *SHP* expression completely surrounds the fruit.



Mutations of the *indehiscent genes ind-1* and *ind-2* produce shatterproof siliques.



Simplified genetic model for the development of the dehiscence zone in Arabidopsis.

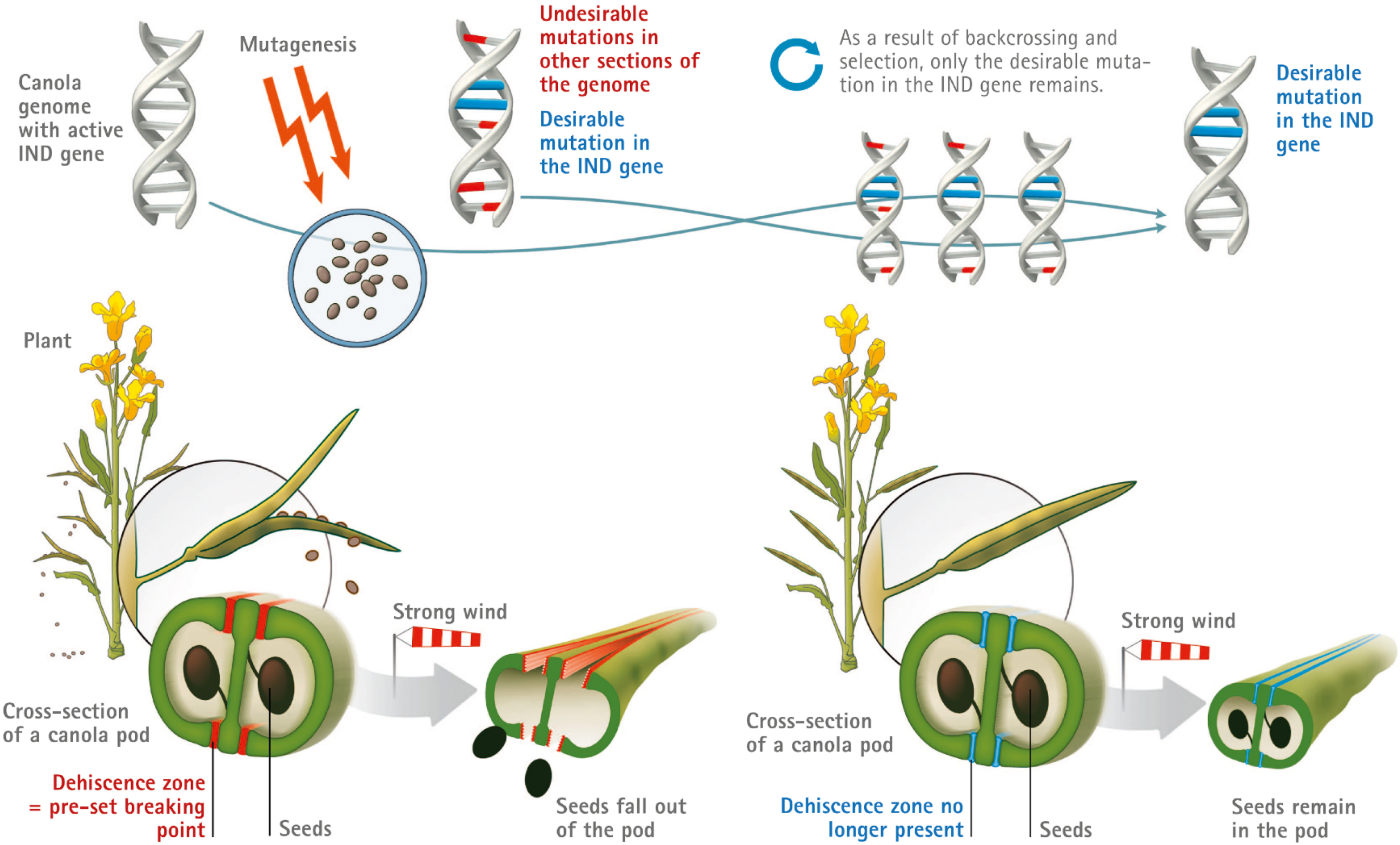
The diagram shows a transverse section across a silique. Valves are shown green, lignified zones: pink, separation layer: blue and replum: yellow.

Fruitful (FUL) and Replumless (REP) limit action of Shatterproof (SHP) to the valve margin. SHP induces Indehiscent (IND) and Alcatraz (ALC) to trigger formation of lignified cells and the separation layer in the dehiscent zone.

Cristina Ferrándiz and Chloé Fourquin, *Journal of Experimental Botany*, Vol. 65, No. 16, pp. 4505–4513, 2014

Strategy for shatter-resistant pods

The stability of the canola pods can be adjusted using reverse genetics. Researchers generate chemical changes (mutations) in the genotype. The candidates with an IND mutation are backcrossed with the original plant. The canola plants that result from this cross have stronger seed pods. The seeds stay in the pod and do not fall out when buffeted by the wind.



Source: *research* – the Bayer Scientific Magazine

InVigor

InVigor® L140P	
Yield	100% of the checks (InVigor 5440 & Pioneer® 45H29) in 2011/2012 WCC/RRC Co-op trials
Days to Maturity	0.5 days earlier than the average of the checks
Growing Zones	All
Lodging Resistance	Strong
Height	Short–Medium
Blackleg Rating	R (Resistant)
Agronomic Trait	LibertyLink®, Pod Shatter Reduction
Overall Comment	The patented pod shatter reduction technology of InVigor L140P offers growers excellent yield protection with greater harvest flexibility. Stronger pod seams and stems firmly adhere to the plant longer and allow seeds to fully mature safely within the pod until harvest. This allows growers to straight cut their canola and maximize yield. In the Demonstration Strip Trial program it showed an 8% yield advantage over normal swath timing.

BAYER

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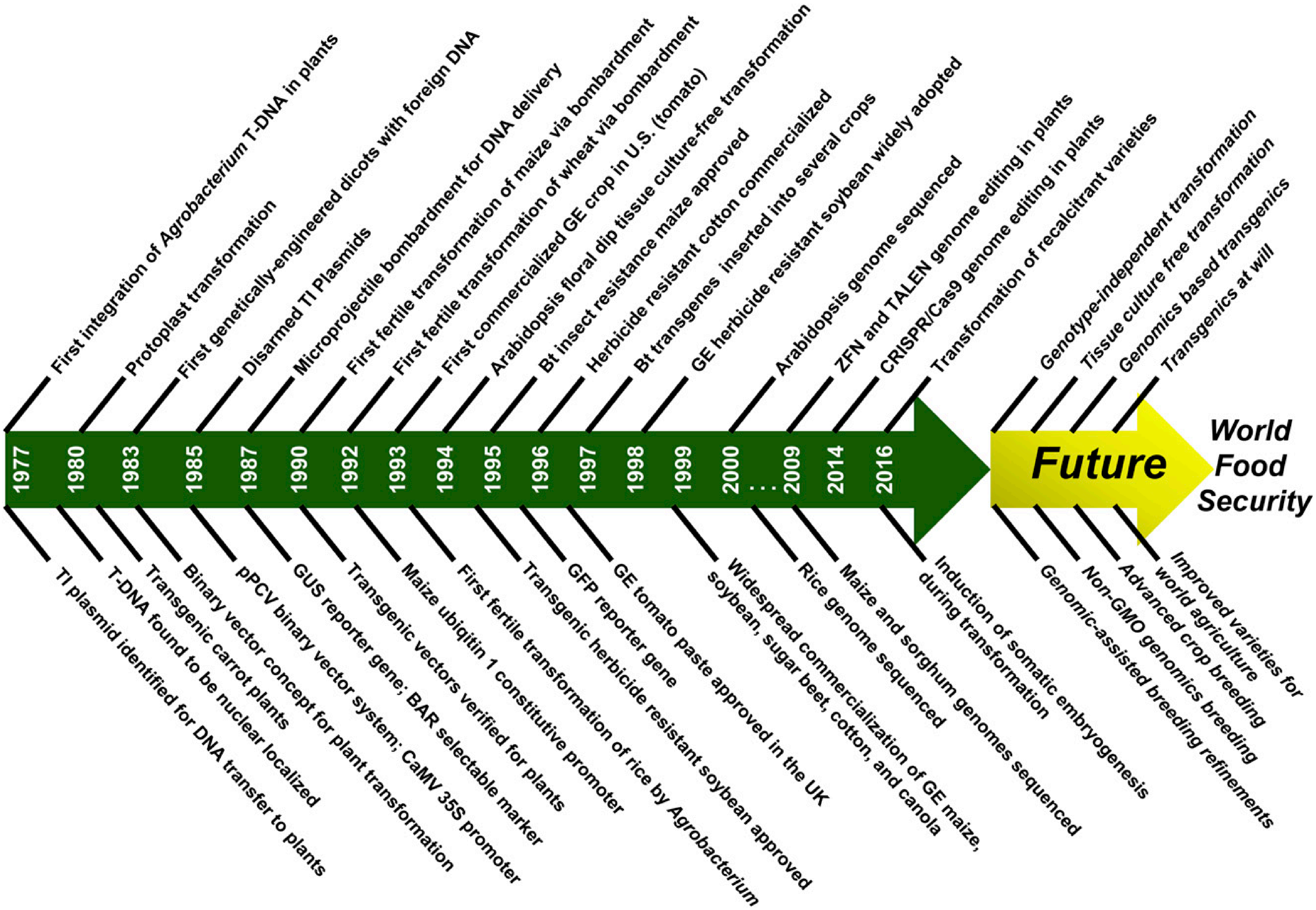
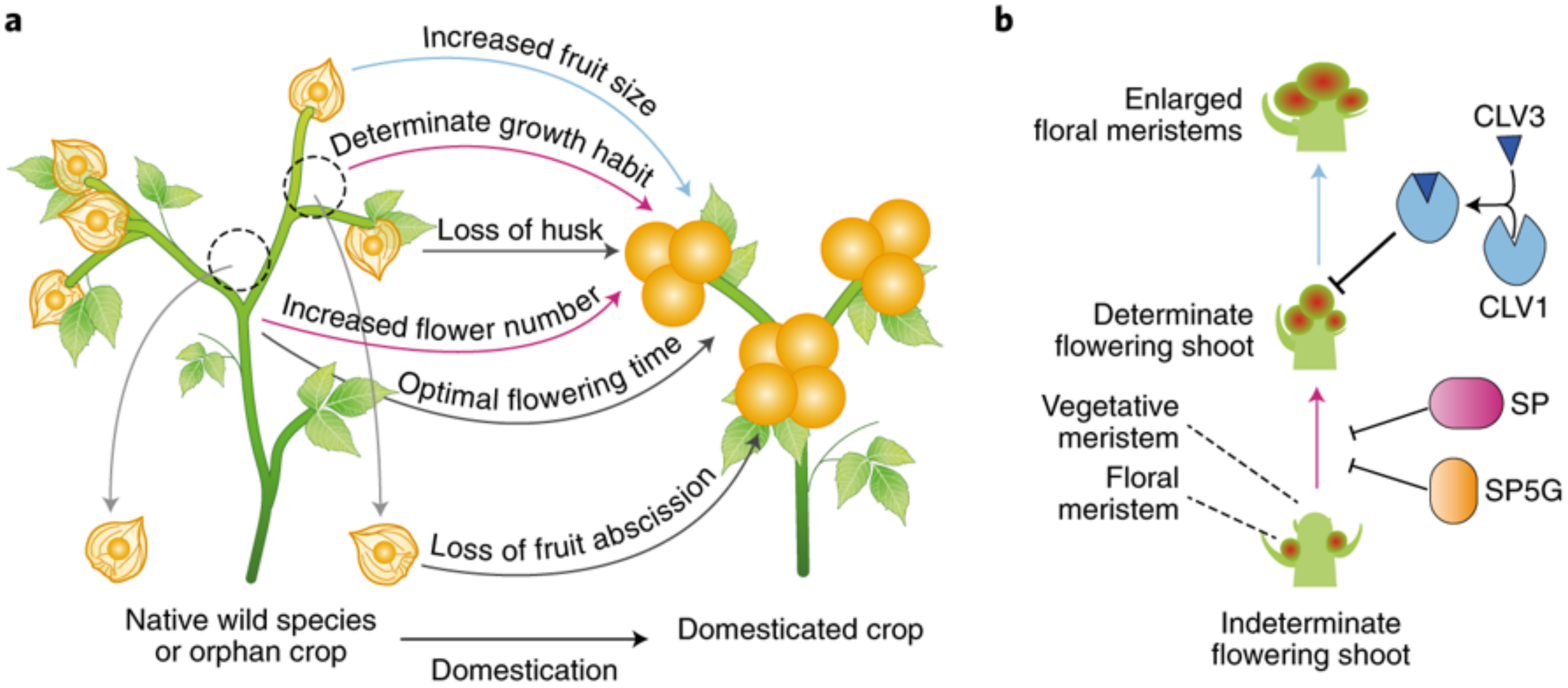
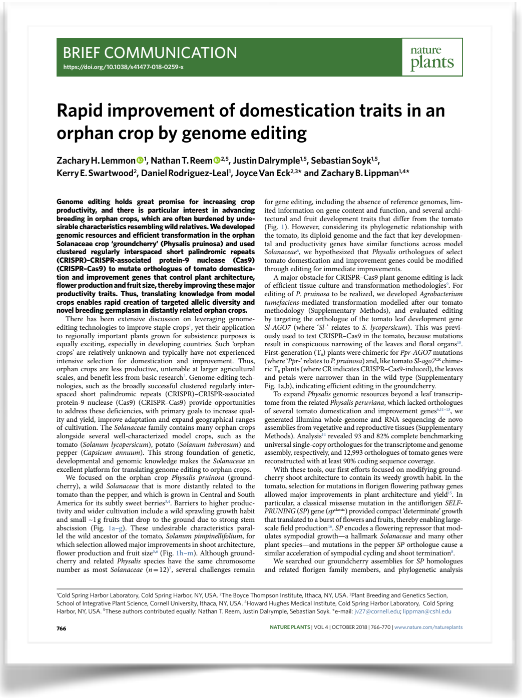


Figure 3. Important Historical Milestones in Plant Transformation.

Since its beginning in 1977, the pace of crop transformation technology development has not been linear. In recent years, the genome editing revolution begs for crop transformation improvements to enable greater food security.





BRIEF COMMUNICATION
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nature plants

Rapid improvement of domestication traits in an orphan crop by genome editing

Zachary H. Lemmon[1], Nathan T. Reem[2,5], Justin Dalrymple[1,5], Sebastian Soyk[1,5], Kerry E. Swartwood[2], Daniel Rodriguez-Leal[1], Joyce Van Eck[2,3]* and Zachary B. Lippman[1,4]*

Genome editing holds great promise for increasing crop productivity, and there is particular interest in advancing breeding in orphan crops, which are often burdened by undesirable characteristics resembling wild relatives. We developed genomic resources and efficient transformation in the orphan Solanaceae crop 'groundcherry' (Physalis pruinosa) and used clustered regularly interspaced short palindromic repeats (CRISPR)–CRISPR-associated protein-9 nuclease (Cas9) (CRISPR–Cas9) to mutate orthologues of tomato domestication and improvement genes that control plant architecture, flower production and fruit size, thereby improving these major productivity traits. Thus, translating knowledge from model crops enables rapid creation of targeted allelic diversity and novel breeding germplasm in distantly related orphan crops.

There has been extensive discussion on leveraging genome-editing technologies to improve staple crops[1], yet their application to regionally important plants grown for subsistence purposes is equally exciting, especially in developing countries. Such 'orphan crops' are relatively unknown and typically have not experienced intensive selection for domestication and improvement. Thus, orphan crops are less productive, untenable at larger agricultural scales, and benefit less from basic research[2]. Genome-editing technologies, such as the broadly successful clustered regularly interspaced short palindromic repeats (CRISPR)–CRISPR-associated protein-9 nuclease (Cas9) (CRISPR–Cas9) provide opportunities to address these deficiencies, with primary goals to increase quality and yield, improve adaptation and expand geographical ranges of cultivation. The *Solanaceae* family contains many orphan crops alongside several well-characterized model crops, such as the tomato (*Solanum lycopersicum*), potato (*Solanum tuberosum*) and pepper (*Capsicum annuum*). This strong foundation of genetic, developmental and genomic knowledge makes the *Solanaceae* an excellent platform for translating genome editing to orphan crops.

We focused on the orphan crop *Physalis pruinosa* (groundcherry), a wild *Solanaceae* that is more distantly related to the tomato than the pepper, and which is grown in Central and South America for its subtly sweet berries[3,4]. Barriers to higher productivity and wider cultivation include a wild sprawling growth habit and small ~1 g fruits that drop to the ground due to strong stem abscission (Fig. 1a–g). These undesirable characteristics parallel the wild ancestor of the tomato, *Solanum pimpinellifolium*, for which selection allowed major improvements in shoot architecture, flower production and fruit size[5,6] (Fig. 1h–m). Although groundcherry and related *Physalis* species have the same chromosome number as most *Solanaceae* ($n=12$)[7], several challenges remain for gene editing, including the absence of reference genomes, limited information on gene content and function, and several architectural and fruit development traits that differ from the tomato (Fig. 1). However, considering its phylogenetic relationship with the tomato, its diploid genome and the fact that key developmental and productivity genes have similar functions across model *Solanaceae*[8], we hypothesized that *Physalis* orthologues of select tomato domestication and improvement genes could be modified through editing for immediate improvements.

A major obstacle for CRISPR–Cas9 plant genome editing is lack of efficient tissue culture and transformation methodologies[9]. For editing of *P. pruinosa* to be realized, we developed *Agrobacterium tumefaciens*-mediated transformation modelled after our tomato methodology (Supplementary Methods), and evaluated editing by targeting the orthologue of the tomato leaf development gene *Sl-AGO7* (where '*Sl-*' relates to *S. lycopersicum*). This was previously used to test CRISPR–Cas9 in the tomato, because mutations result in conspicuous narrowing of the leaves and floral organs[10]. First-generation (T_0) plants were chimeric for *Ppr-AGO7* mutations (where '*Ppr-*' relates to *P. pruinosa*) and, like tomato *Sl-ago7*^{CR} chimeric T_0 plants (where CR indicates CRISPR–Cas9-induced), the leaves and petals were narrower than in the wild type (Supplementary Fig. 1a,b), indicating efficient editing in the groundcherry.

To expand *Physalis* genomic resources beyond a leaf transcriptome from the related *Physalis peruviana*, which lacked orthologues of several tomato domestication and improvement genes[6,11–13], we generated Illumina whole-genome and RNA sequencing de novo assemblies from vegetative and reproductive tissues (Supplementary Methods). Analysis[14] revealed 93 and 82% complete benchmarking universal single-copy orthologues for the transcriptome and genome assembly, respectively, and 12,993 orthologues of tomato genes were reconstructed with at least 90% coding sequence coverage.

With these tools, our first efforts focused on modifying groundcherry shoot architecture to contain its weedy growth habit. In the tomato, selection for mutations in florigen flowering pathway genes allowed major improvements in plant architecture and yield[15]. In particular, a classical missense mutation in the antiflorigen *SELF-PRUNING* (*SP*) gene (*sp*^{classic}) provided compact 'determinate' growth that translated to a burst of flowers and fruits, thereby enabling large-scale field production[16]. *SP* encodes a flowering repressor that modulates sympodial growth—a hallmark *Solanaceae* and many other plant species—and mutations in the pepper *SP* orthologue cause a similar acceleration of sympodial cycling and shoot termination[8].

We searched our groundcherry assemblies for *SP* homologues and related florigen family members, and phylogenetic analysis

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news & views

CROP ENGINEERING

The taming of the shrub

Can genomics, functional analysis and genome editing help build the bridge between orphan crops and modern agriculture?

Luca Comai

The world's food supply depends on a few crop species, such as rice, wheat, maize, soy and potato, on which research and breeding efforts are concentrated. In addition, small farmers grow a variety of orphan crops, a set of species that are tasty, nutritious and well adapted, but mostly unsuited for intensive agriculture because of their wild characteristics. In this issue of *Nature Plants*, Lemmon et al.[1] edit the genome of orphan crop *Physalis pruinosa* (groundcherry) to explore domestication of this species. Specifically, they modify genes whose orthologues control domestication traits in the close relative, tomato. The authors' results demonstrate both the power of this approach and the importance of identifying mechanisms and gene targets. Thanks to genetic and genomic analyses[2], the path to domestication from wild ancestor to modern crop is becoming clearer for several cultivated species. Evidence indicates that mutations altering the function of a few, selected loci, called domestication genes, played a determining role. For example, alleles at a few major loci are responsible for much of the difference between wild teosinte and modern maize[2]. Domestication genes have been identified in other key crop species: they control flowering and fruit development, increase harvest index (more product per plant), facilitate harvesting by inhibiting abscission of fruits, or make the final product easier to store, chew and digest[2]. Manipulation of these traits stands as one of the great human achievements. Some traits, such as loss-of-shattering, were unknowingly selected by Neolithic gatherers. Other traits, such as branching and determinate growth, required keen observation and intent to save the variant. By increasing food availability, crop domestication has enabled the flourishing of sciences, arts and technology. While the basic chassis of our staple species is Neolithic, some improvements are recent, such as semi-dwarfism in wheat and rice. Notably, tomato was radically altered to enable mechanical harvesting by combining a spontaneous mutation in *SELF-PRUNING* (Fig. 1)[3] with alleles of other genes that make the fruit hard to bruise and rich in solids[2].

The availability of genomic information and efficient genome editing tools represents a novel opportunity for crop domestication and improvement[2,4]. Wild species and unimproved orphan crops can now, in theory, be modified rapidly and in a targeted manner, to provide novel and improved crops. Consider groundcherry (*P. pruinosa*), a solanaceous species that produces a small, but tasty berry. A garden curiosity[5], groundcherry cannot be grown on an agricultural scale because of wild characteristics such as sprawling habit, small, husked fruit and strong fruit abscission. The growth habit and production of small fruits unsuited for agriculture resemble the characteristics of the wild 'currant' tomato *Solanum pimpinellifolium*, which was domesticated to become tomato. Lemmon and co-workers saw an opportunity: would modification of the known gene targets of tomato domestication achieve corresponding gains in this sister species? Through gene editing, they targeted repressors of the florigen pathway to increase flower numbers and delimit flowering time, both on primary and axillary shoots. Knockout of *SELF-PRUNING*, a classical improvement gene that controls indeterminate versus determinate growth in tomato, was too severe to be useful, resulting in extreme compactness. Knockout of another florigen repressor, *SP5G*, resulted in increased axillary flowering, although caused no changes to the primary shoot; nonetheless, fruit density increased. The authors next targeted the CLAVATA pathway, which regulates shoot apical meristem size by the interaction of a small peptide, CLV3, with its receptors (CLV1 and others). Knockout of *CLV1* resulted in increased flower meristem size, additional flower organs and conversion from two-locule to a larger, three-locule fruit. These manipulations produced variants better suited to, although well short of, full agricultural exploitation and constitute an impressive demonstration of what is possible through a combination of genomics and gene editing of just a small number of loci.

The study, as successful as it was, also demonstrates the challenges that 'domesticators' will encounter. Domesticating an orphan crop plant requires multiple tools: a well elucidated genome sequence, including the understanding of paralogue structure and gene expression, and a delivery system for genome editing, the simplest being a transformation system. Just as important is the ability to predict what targeted modification will achieve the ideal phenotype. Target identity can be inferred by understanding the domestication history of crops closely related to the orphan crop. Nonetheless, the structure of gene networks varies according to node number, type and connections[6]. A change yielding the desired outcome in one species may be too severe, insufficient or completely devoid of effect in another. Breeders and geneticists have long known that genetic modifiers present in populations can dramatically alter a mutation phenotype. This was demonstrated here by the dwarfing effect of the *SELF-PRUNING* knockout in groundcherry, or by the inability to modify primary shoot flowering by SP5G manipulation. In many cases, a knockout may be inadequate and a subtler allele may be needed instead, such as altering promoter activity or protein structure. Editing promoter segments should facilitate the production of alleles with new and useful expression properties[7]. Finally, the accelerated domestication envisaged here may involve manipulation of several genes with the connected combinatorial challenge of testing many variables. In fact, it is possible that domesticated species may owe their fate in part to their relative ease of genetic manipulation: if key domestication traits were monogenic and variable in the ancestor, they would have been easily apparent and selectable by breeders. Orphan crops, in contrast, may have resisted domestication because of multigenic regulation of the same traits[8]. All things considered, what are the prospects for 'taming wild species'? The work by Lemmon et al.[1]

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Rapid improvement of domestication traits in an orphan crop by genome editing.

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